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Systematic Review and Phylogenetic Analysis of the Nudibranch Genus *Melibe* (Opisthobranchia: Dendronotacea) with Descriptions of Three New Species

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Three new species of the genus *Melibe* are described: *Melibe digitata* sp. nov. and *M. tuberculata* sp. nov. are recorded from the Philippines. Specimens of *M. minuta* sp. nov. have been found only from Okinawa, Japan. Specimens of *Melibe engeli* Risbec, 1937 are recorded and described from the Hawaiian Islands and the Philippines and an additional photo is noted from southern Japan. These represent the first published records of this species since its original description. The anatomy of an additional nine species of *Melibe* is re-examined. These include: *M. australis* (Angas, 1864), *M. bucephala* Bergh, 1902, *M. leonina* (Gould, 1852), *M. liltvedi* Gosliner, 1987, *M. megaceras* Gosliner, 1987, *M. papillosa* (de Filippi, 1867), *M. pilosa* Pease, 1860, *M. rosea* Rang, 1829 and *M. viridis* (Kelaart, 1858). Consistent anatomical differences suggest that *M. pilosa* and *M. papillosa* represent distinct species. This review of the morphological variability within the genus provides the basis for a phylogenetic analysis of the group. *Melibe* is shown to represent a monophyletic clade. Members of the genus *Tethys* represent the sister group of *Melibe*.

The dendronotacean genus *Melibe* Rang, 1829 is one of two genera comprising the family Tethydidae. Several of these species are known only from their original descriptions, and most species have been only superficially described with an emphasis on external anatomy. Gosliner (1987) reviewed aspects of the systematics and anatomy of *Melibe* and described two new species. He considered the genus as containing 15 valid species from throughout the world. Collections of three apparently undescribed species from the Philippines and Okinawa have prompted a review of the genus to provide data for adequate morphological comparison as well as evidence for constructing a phylogenetic hypothesis of relationships within the family and genus. Specimens of nine additional species were examined to amplify previous descriptions and examine characters for phylogenetic analysis. In cases where portions of the anatomy have been described elsewhere, only new information or data that do not agree with previous descriptions are included here.

Species Descriptions

Family Tethydidae Rafinesque, 1815

Genus *Melibe* Rang, 1829

Type species: *Melibe rosea* Rang, 1829, by monotypy.

Synonyms.— *Chiroraera* Gould, 1852 (type species: *C. leonina* Gould, 1852). *Jacunia*

Filippi, 1867 (type species: *J. papillosa* Filippi, 1867). *Melibaea* Angas, 1864 (type species: *M. australis* Angas, 1864). *Meliboea* Kelaart, 1858 (type species: *M. viridis* Kelaart, 1858). *Propomelibe* Allan, 1932 (type species: *P. mirifica mirifica* Allan, 1932).

Melibe australis (Angas, 1864)

Melibaea australis Angas, 1864:62, pl. 6., fig. 2.
Melibe australis (Angas, 1864) Burn, 1957. Wells and Bryce, 1993:174, fig. 225. Debelius, 1996:228, middle fig.

MATERIAL EXAMINED.— Natural History Museum, London, BMNH 1965400, 8 specimens, Torkay and Point Londsdale, Victoria, Australia, 1 January, 1965, R. Burn.

DISTRIBUTION.— Known from New South Wales, Victoria, Tasmania and Western Australia, Australia (Angas 1864; Burn 1957; Wells and Bryce 1993; Debelius 1996).

EXTERNAL MORPHOLOGY.— The preserved specimens examined here are small, up to 7 mm in length. The body surface is covered with low tubercles. The oral hood is relatively small and smooth with only a single row of tentacles along the margin. Papillae are absent from the outer surface of the hood, but are present on the inner surface around the mouth. The rhinophores are well separated and lack papillae or posterior ornamentation on the rhinophore sheath. The foot is narrow and linear without papillae on the anterior margin. The cerata are globular with irregular low tubercles. The genital opening lacks papillae around the aperture.

DIGESTIVE SYSTEM.— The buccal mass is wide, but is devoid of jaws or salivary glands. The esophagus is short and widens into the stomach, which lacks any chitinous plates. The anterior digestive gland is a compact mass that surrounds the stomach, but none of its ducts enter the cerata. The posterior gland is also compact and none of its ducts enter the cerata.

CENTRAL NERVOUS SYSTEM.— The ganglia are all smooth and rounded, devoid of tubercles. The cerebral and pleural ganglia are fused. The pedal commissure is elongate. The buccal ganglia are well separated.

REPRODUCTIVE SYSTEM.— The reproductive system was not well preserved and probably was not fully mature in the small animals examined here. The compound ovotestis follicles form a solid mass.

DISCUSSION.— From the subsequent phylogenetic analysis, it appears that *Melibe australis* is the sister species to all of the Indo-Pacific species. *Melibe australis*, like other members of the larger clade to which it belongs, has a small oral hood that has been secondarily enlarged in some members of the clade, a papillate mouth surface and a relatively narrow foot, that has been secondarily widened in some members of the clade. *Melibe australis* has two autapomorphic features: loss of stomach plates and salivary glands.

Melibe bucephala Bergh, 1902

(Fig. 2a–d)

Melibe bucephala Bergh, 1902:205, pl. 3, figs. 6–10. O'Donoghue, 1929:803, fig.220. Debelius, 1996:286, bottom fig., 287.

MATERIAL EXAMINED.— Natural History Museum, London, BMNH 1933.6.30.35, 1 specimen, Suez Canal, H. M. Fox. This is the same specimen described by O'Donoghue (1929).

DISTRIBUTION.— Known from Thailand (Gulf of Siam) (Bergh 1902) and the Red Sea (O'Donoghue 1929; Debelius 1996).

External morphology.— Living animals may reach 100 mm (Debelius 1996). The preserved specimen examined is large, 40 mm in length. The body is elongate, limaciform, and somewhat compressed anterolaterally, with a slightly elevated dorsal hump in the cardiac region and tapering gradually to a slender posterior portion of the foot. Rounded to slightly conical papillae are present on the notum and cerata. The papillae on the body are smaller than those on the cerata. The wide, linear foot has a rounded, entire, anterior margin, which becomes somewhat undulate on the lateral portions. There are no papillae proximal to the anterior portion of the foot. The oral hood is large with anteriorly and posteriorly incised margins. The margin of the hood has three to five rows of cylindrical papillae, which taper to conical points, with the innermost row the longest. There are scattered papillae on the surface of the oral hood. The well-separated perfoliate rhinophores have 6 to 7 lamellae and arise from the surface of the oral hood within cylindrical sheaths. Extending from the posterior portion of the sheath is a laterally compressed, posteriorly directed sail, which bears low tubercles and terminates in an apical papilla. There are six cerata per side of the body. They are somewhat flattened, saccate, oval to triangular with a papillate surface. The anus is located immediately anterior to the second ceras on the right side of the body. The nephroproct is dorsal and slightly posterior to the anus. The gonopore is on the right side of the body below and slightly anterior to the first ceras. A circle of 14 small, conical papillae surrounds the gonopore.

Digestive System.— (Figs. 2b,d) The coarsely papillate interior of the oral hood connects with the elevated, papillate mouth. The buccal mass had previously been removed, but was recorded by O'Donghue (1929) as being devoid of a radula, but containing a pair of chitinous jaws with an undulate border. The surface of the remains of the buccal mass is papillate. A pair of elongate nodular salivary glands lies on either side of the middle portion of the buccal mass. The short, wide esophagus emerges from the posterior of the buccal mass and expands into the saccate, muscular stomach. The posterior portion of the stomach contained 24 triangular, chitinous plates, with thin, eccentric apices arranged in an alternating manner. The plates also alternate between large and small in size. The intestine leaves the posterodorsal portion of the stomach and curves dorsally, straightening and ending at the anus. A branch of the diffuse digestive gland originates from the right side of the stomach and ramifies into more than half of the basal portion of the first anterior ceras on the right side. A large branch of the digestive gland originates from the posterolateral portion of the stomach on the left side, proximal to the entrance of the esophagus into the stomach. Bifurcating immediately after its emergence from the stomach, this branch ramifies into more than half of the length of the anteriormost ceras on the left. The anterior portions of the digestive gland also ramify around the stomach. The remaining elongate branch spreads posteriorly, interdigitating with the ovotestis and ramifying into most of the length of the next two pairs of posterior cerata. Posteriorly from this point the branch continues to ramify posteriorly, but does not enter into any of the remaining cerata.

Central nervous system.— The ganglia are not entirely intact, but it is evident that the cerebral, pleural and pedal ganglia are almost entirely separate but are situated in close proximity to each other. All of these ganglia have a granular appearance caused by the presence of distinct, peripheral, globular nerve cells (Fig. 2c). An elongate commisure joins the pedal ganglia. The paired buccal ganglia lie adjacent to each other on the ventral surface of the esophagus, and are connected to the pedal ganglia by paired nerves. Each buccal ganglion is smooth.

Reproductive system.— The dissected specimen has more than 20 compound, spherical, congested ovotestis bodies (Fig. 2d). The narrow preampullary duct widens and enters the s-shaped ampulla posteriorly (Fig. 2a). The ampulla constricts slightly before forming the distal portion, which branches into the oviduct and vas deferens. The slender vas deferens enters almost immedi-

ately into the spherical prostate before exiting, enlarging, and making a bend before penetrating the bulbous proximal end of the conical penis, which lies within the penial sac. The distal end of the penial papilla is curved. The penial sac terminates proximally to the gonopore. The large, smooth mucous gland comprises most of the female gland mass, along with the nodular albumen gland and folded membrane gland. The proximal oviduct is undulate, probably serving as a serial receptaculum seminis, based on its position and thicken muscularized structure. The oviduct bifurcates, one branch expanding into a pyriform bursa copulatrix, the other leading to the vagina. A distinct banded vaginal gland is present internally around the vagina (Fig. 2a).

Discussion.— *Melibe bucephala* appears to be the sister species of *M. viridis*. These species share two synapomorphies. Both have a coarsely papillate inner surface of the oral hood and a wide foot. *Melibe bucephala* has two autapomoprhies: an absence of ceratal papillae and a papillate buccal mass

***Melibe digitata* Gosliner and Smith, sp. nov.**
(Figs. 1a, 3–5)

Type material.— Holotype: CASIZ 106449, one specimen, collected at 10 m depth, Devil's Point, Maricaban Island, Batangas Province, Luzon, Philippines, 15 April, 1996, T.M. Gosliner. Paratypes: CASIZ 103754, six specimens, with egg mass, collected at 10 m depth, Pinnacle Rock, Hamilo Bay, Batangas Province, Luzon Island, Philippines, 4 March 1995, T.M. Gosliner. CASIZ 096242, two specimens, with egg mass, collected at 12 m depth, Devil's Point, Maricaban Island, Batangas Province, Luzon Island, Philippines, 14 March 1994, T.M. Gosliner. CASIZ 103756, twelve specimens, with egg mass, collected at 1 meter depth, Bonito Island, Maricaban Island, Batangas Province, Luzon, Philippines, 27 February, 1995, T.M. Gosliner. CASIZ 110380, two specimens, collected at 2 m depth, Cemetery Beach, Maricaban Island, Batangas Province, Luzon, Philippines, 19 April, 1997, T.M. Gosliner. CASIZ 110425, four specimens collected at 12 m depth, Devil's Point, Maricaban Island, Batangas Province, Luzon, Philippines, 20 February, 1997, T.M. Gosliner.

Distribution.— Thus far, specimens of *Melibe digitata* have been found on several occasions in the Batangas Province of the Philippines in the vicinity of Maricaban Island and Hamilo Bay. This species has not been found from other localities.

Etymology.— The name *digitata* refers to the highly digitate branching of the cerata.

External Morphology.— The color of the living animals is creamy white to greenish brown, with darker green coloration towards the distal ends of the cerata. The animal is translucent or semi-transparent and the viscera are readily visible through the surface of the living and preserved animals (Fig. 1a). The preserved specimens reach a maximum length of 25 mm. The body is limaciform, somewhat compressed anterolaterally, and is elevated dorsally in a hump at the midbody region. Posterior to the hump, the body tapers abruptly into a narrow posterior portion of the foot (Fig. 3a). The notum is smooth, with a scattering of very fine white glandular dots or tubercles. The foot is more opaque, narrow and linear with the anterior margin rounded and entire. The remainder of the margin is somewhat undulate. There are one to five small conical papillae on or immediately proximal to each side of the anterior foot margin. The oral hood is small relative to the body, (6 mm in diameter for the largest specimen) and is produced from a distinctly narrowed base. The hood is semi-transparent, and has many very fine whitish glandular dots or tubercles over its surface. The partially opaque hood margin has an inner and outer row of narrowly tapering tentacular papillae with acute or acuminate apices. The tips of the inner row tend to be curled, and the two rows are of equal length. The dorsal hood surface has from 10–20 larger and less acutely taper-

ing papillae that are denser near the margin. In many of the specimens one or two of these papillae were bifid or trifid. The perfoliate rhinophores (Fig. 3b) have 5–7 lamellae and are born within long cylindrical sheaths arising close together from the narrow portion of the body posterior to the hood. The length of the sheaths is nearly equal to the hood diameter. The distal margin of the sheath thickens and expands to produce a coronate row of 5 to 11 short papillae on the anterior margin, and a single fingerlike papilla on the posterior margin, which may exceed the length of the exposed rhinophore. The arborescent, inflated cerata arise from cylindrical bases, and reach aproximately 2/3rds of the body length (Fig. 3c). The basal 2/3rds of the cerata are unbranched or have few simple branches. The distal portions are highly ramified and terminate in multifid acutely tapering apices. The basal portions are semi-transparent and colored like the notum, but the ramified portions are more opaque, and in the living animal (Fig. 1a) exhibit a pronounced greenish-brown coloration probably denoting the presence of zooxanthellae. There are 4–7 cerata per side arranged close to the midline of the dorsum. The anteriormost cerata are opposite, with the remainder alternating. The posteriormost few cerata are smaller with less developed branching. The anus is located just anterior to the second right ceras. The nephroproct is just dorsal to the anus. The gonopore is well ventral to the most anterior right ceras, near the lateral midline of the body. Many of the observed specimens have one or two conical papillae ventral to the anteriormost right ceras, proximal to the gonopore.

Digestive System.— The finely papillate inner surface of the oral hood connects to the raised, papillate mouth, which opens into a muscular buccal mass (Fig. 4b). The buccal mass is of intermediate width compared with the other new species described. The mass is devoid of a radula, but a pair of chitinous jaws with a smooth masticatory margin is present (Fig. 5a). A pair of elongate salivary glands is present near the middle of either side of the buccal mass. An elongate esophagus emerges from the posterior end of the buccal mass and expands into the muscular saccate stomach. In one dissected specimen, the posterior portion of the stomach contained 17 thin triangular plates of subequal size with their eccentric apices arranged in an alternating fashion (Figs. 5b, c). The intestine is produced from and is contiguous with the posterodorsal portion of the stomach, curving posteriorly before recurving slightly to the anal opening. The diffuse digestive gland originates from the lateral portion of the stomach, is relatively compact and undeveloped posteriorly, and covers the surface of the ovotestis in an undulating fashion. A separate branch comes from the right side of the stomach and ramifies into the anteriormost right ceras. A branch on the left side of the stomach ramifies into the remaining cerata.

Central nervous system.— The smoothly textured cerebral and pleural ganglia are fused, and are connected by a short commissure to the smaller pedal ganglia (Fig. 4b). The eyes are situated at the end of short nerves that join them to the dorsal surface of the cerebral ganglia. The small, spherical buccal ganglia are situated on the ventral surface of the buccal mass in such a way that they touch each other, and are joined to the cerebral ganglia by thin, short nerves.

Reproductive system.— The arrangement of the reproductive system is triaulic (Fig. 4a). Seven compactly congested ovotestis follicles were found in one specimen dissected, and were held together by the digestive gland branches on the surface of each. The narrow preampullary duct enters the dorsal portion of the proximal lobe of the relatively large, bilobed, saccate, inflated ampulla. The ampulla narrows briefly before expanding to form the second lobe that narrows distally, bifurcating into the oviduct and the vas deferens. The oviduct widens into a serial, fan-shaped receptaculum seminis, narrows again forming two convolutions and widens slightly before entering the pyriform bursa copulatrix. Proximal to its exit is a duct that joins the vagina at the proximal end, where a compact mass of nodular globules forms a distinct vaginal gland. The female gland mass is composed of a large, smooth mucous gland, and the smaller membrane and albumen

glands. After exiting the ampulla, the narrow vas deferens enters almost immediately into the relatively large, spherical prostate, which is composed of many small globose bodies. Exiting the prostate, the vas deferens makes several bends before entering the base of the relatively short, conical penis. The penis is within the penial sac, which then joins with the vagina at the genital opening.

DEVELOPMENT.— A flatly coiled whitish egg ribbon arranged as a three-tiered spiral whorl was also found. It contained numerous clear gelatinous capsules approximately 0.12 mm in diameter, each with a single opaque white egg.

NATURAL HISTORY.— The species has been found in 1–12 meters of water. Specimens are generally found on or under the surface of rounded basaltic stones, and have been found on two occasions with specimens of *Melibe tuberculata.*

DISCUSSION.— *Melibe digitata* can readily be distinguished from other members of the genus by its highly ramified cerata. Its golden greenish to brownish body color makes individuals of this species highly cryptic in its natural environment, and probably denotes the presence of zooxanthellae. *Melibe digitata* appears to be the sister species of *M. tuberculata* according to the subsequent phylogenetic analysis. The two species share numerous apomorphies. In both species the rhinophores are inserted close to each other basally and the serial receptaculum seminis is expanded. Both species have a secondarily smooth body and smooth jaws. In both taxa, the rhinophoral sail and ceratal tubercles appear to have been secondarily lost and the number of stomach plates is less than 20. Both species have a poorly developed posterior digestive gland.

Melibe digitata differs from *M. tuberculata* in several significant regards. The most obvious difference between the two is the presence of acutely pointed papillae in *M. digitata* versus rounded papillae in *M. tuberculata.* The bursa copulatrix of *M. digitata* is pyriform whereas in *M. tuberculata* it is more spherical. The ovotestis follicles of *M. digitata* are close to each other whereas in *M. tuberculata* they are well separated. In *M. digitata* the digestive gland enters more than half of the ceratal length, whereas in *M. tuberculata* the gland is only found in the basal half. In *M. digitata* the buccal mass is moderately narrow, while in *M. tuberculata* it is much wider. The salivary glands are elongate in *M. digitata* and much shorter in *M. tuberculata.* The pleural ganglia of *M. digitata* are largely fused while in *M. tuberculata* they are well separated.

Melibe engeli Risbec, 1937

(Figs. 1d, 6–9)

Melibe engeli Risbec, 1937:160. Risbec, 1953:114, fig. 68 a–g. Catala, 1986:83, fig. 30.

MATERIAL EXAMINED.— CASIZ 105680, one specimen, collected at 12 m depth, The Head, Hamilo Bay, Batangas Province, Luzon Island, Philippines, 4 March, 1995, M. Miller. CASIZ 085887, one specimen, collected at 23 m depth, Layaglayag Point, N.W. side of Maricaban Island, Batangas Province, Luzon, Philippines, 22 March 1993, T.M. Gosliner. CASIZ 096241, one specimen, collected at 4 m depth, Seafari Beach, Anilao, Batangas Province, Luzon Island, Philippines, 17 March 1994, T.M. Gosliner. CASIZ 106396, one specimen, collected at 2 m depth, Cemetery Beach, Maricaban Island, Batangas Province, Luzon, Philippines, 15 April 1996, T.M. Gosliner. CASIZ 110389, four specimens, collected at 2 m depth, Cemetery Beach, Maricaban Island, Batangas Province, Luzon, Philippines, 20 April 1996, T.M. Gosliner. CASIZ 093685, one specimen, collected at 20 m depth, in an algal mat, Makena, Maui, Hawaii, 16 January 1993, M. Severns. CASIZ 089652, three specimens, collected at 1 meter depth, on *Acanthophora spicifera* at night, Hekili Point, Maui, Hawaii, 26 September, 1993, C. Pittman. CASIZ 093678, two speci-

mens, collected in low intertidal on *Acanthophora spicifera*, Hekili Point, Maui, Hawaii, 16 October 1993, C. Pittman. CASIZ 093676, three specimens, collected in shallow subtidal, Hekili Point, Maui, Hawaii, 11 October, 1993, C. Pittman.

Distribution.— This species has been recorded from New Caledonia (Risbec, 1937, 1953; Catala, 1986 and has most recently been collected from Japan (A. Ono, pers. commun., http://online.divers.ne.jp/ono/seaslug3/room3-12.html), Hawaii (present study) and the Philippines (present study).

External morphology.— The living animals are virtually transparent, with a slight greenish yellow coloration and white and cream colored internal organs (Fig. 1d). The preserved specimens reach a maximum of 30 mm in length and are white to pale yellow, extremely transparent, with the internal organs and muscle fibers clearly visible (Fig. 6a). The body is limaciform and elongate, somewhat compressed anterolaterally, tapering posteriorly into a narrow rounded posterior portion of the foot. The body surface has few to many conical papillae, tapering to acute or acuminate apices. There are scattered fine white dots or tubercles on or near the body surface, which are more numerous on the papillae. The foot is narrow and linear, opaque white, with the anterior margin rounded and entire. There are 2–4 small conical papillae tapering to acute or acuminate apices on or proximal to the anterior margin of the foot. The circular oral hood is small compared to the rest of the body. The margin of the hood is entire in the majority of the specimens observed, although in some it is indented slightly, usually basally. In all specimens there is an inner and an outer row of long, tapering, conical, tentacular papillae with recurving tips. These are most often found in an opposite arrangement, but may also be found alternating. Some specimens exhibit up to 5 rows, most often near the basal margin. These rows are more or less equal in length, and have a visible axial fiber extending from the hood margin out to the tip, and a concentration of fine white spots. There are additional papillae on the dorsal surface of the hood, generally resembling those on the body surface, and more concentrated towards the anterior margin. The rhinophores are sheathed and born within separated processes that arise from the dorsal surface of the oral hood (Fig. 6b). The sheaths are somewhat inflated and cylindrical with spreading circular margins that produce a flattened, leaf-like posterior process. There is a great deal of variation among specimens, but a "cockscomb" of 3–5 obtuse to acutely pointed papillations is typical present, creating an effect that resembles the outline of a typical ceras. The cerata are inflated, and variable in outline, ranging from oval, saccate, or pyriform, to elongate and cylindrical (Fig. 6c). The surface may be smooth, or covered with low tubercles that give it a broadly warty look, or that may give the margins a lobed or undulating appearance. In the living animals these may appear more papillate (Fig. 1d). The distal margins range from plain and oval to papillately ornamented. The ornamentation may range from low obtuse papillae to one to three flattened processes bearing 3–6 elongate triangular pappilae in a "cockscomb" pattern. This wide range of variability may be due in part to the dehiscence or autotomy of the cerata at the basal end. Specimens have been observed with few to many missing cerata, and with cerata in different stages of apparent regeneration and growth. The cerata are transparent, and the branches of the digestive gland within them are visible. There are fine white spots or tubercles, possibly glandular in nature, visible on the surface of the cerata, and concentrated on the margins and the papillae. There are 3–6 cerata on each side of the dorsal midline. The anteriormost left and right cerata are opposite, with the remaining cerata most often alternating. The anus is located on the right side in the gap between the first and second anterior cerata, midway or slightly more proximal to the anteriormost ceras. The nephroproct is immediately dorsal to the anus. The gonopore is well ventral to and on a line with or just anterior to the anteriormost right ceras. There are no papillae associated with the gonopore.

Digestive system.— The finely papillate interior of the oral hood connects with the slightly

elevated, papillate mouth. The buccal mass is wide and muscular, devoid of a radula, but containing a pair of denticulate, chitinous jaws (Figs. 9a–b). A pair of compact, nodular salivary glands lies on either side of the middle portion of the buccal mass (Figs. 7a–b). The narrow, elongate esophagus emerges from the posterior of the buccal mass and expands into the saccate, muscular stomach. The posterior of the stomach contained triangular, chitinous plates, with thickened, eccentric apices arranged in an alternating manner (Figs. 9c–d). The plates also alternate between large and small in size. In the present study, one specimen dissected contained 15–16 plates, and the other contained 22. The intestine leaves the posterodorsal stomach and curves dorsally, straightening and ending at the anus. A branch of the diffuse digestive gland originates from the right side of the stomach and ramifies well into the first anterior ceras on the right side. Another large branch of the digestive gland originates from the posterolateral side of the stomach on the left side, proximal to the entrance of the esophagus into the stomach. Bifurcating immediately, a branch ramifies into the anteriormost ceras on the left. The remaining elongate branch spreads posteriorly, interdigitating with the ovotestis and ramifying into the remaining cerata.

Central nervous system.— The cerebral and pleural ganglia are smooth and fused (Figs. 7a–b). They are joined to the pedal ganglia by a short commisure. A short pedal commissure joins the pedal ganglia. A pair of nerves joins with each of the small, spherical buccal ganglia lying on the ventral esophagus, touching each other. The small, dark eyes are situated on anterodorsal portions of the cerebral ganglia.

Reproductive system.— The dissected specimen has 9 simple, spherical, well separated ovotestis bodies (Fig. 7a). The narrow preampullary duct enters the saccate ampulla ventrally (Figs. 8a–b). The ampulla constricts slightly before forming the distal portion that then branches into the oviduct and vas deferens. The slender vas deferens enters almost immediately into the spherical prostate. It then exits from the prostate, enlarges, and makes a bend before penetrating the bulbous proximal end of the conical penis, which lies within the penial sac. The penial sac terminates proximally to the gonopore. The large, smooth mucous gland comprises most of the female gland mass, along with the nodular albumen gland and folded membrane gland. The proximal oviduct widens slightly before forming an "S" curve, which probably serves as a serial receptaculum seminis. The oviduct bifurcates, one branch expanding into a pyriform bursa copulatrix, the other leading to the vagina. A distinct, nodular vaginal gland lies alongside the vagina. In one of the dissected specimens, a distinct muscular band was observed around the neck of the vagina, just distal to the vaginal gland and proximal to the terminus of the penial sac.

Natural history.— This species has been found under rocks and on clumps of the brown alga *Padina* sp., as well as on *Acanthophora* sp.

Discussion.— *Melibe engeli* has only been recorded from the type locality, New Caledonia. These new records from Hawai'i and the Philippines represent significant range extensions. This species is remarkable by its transparent body and may easily be overlooked in the field. Specimens studied do not differ markedly from those described by Risbec (1937, 1953). This species appears to be the sister species to *M. digitata* and *M. tuberculata*. These three species share six synapomorphies. All three species have a series of papillae situated immediately dorsal to the anterior end of the foot. The papillae of the oral hood are equal in length in *M. digitata, M. engeli* and *M. tuberculata*. In these taxa the esophagus is elongate, the digestive gland is ramified only within the cerata and the pedal commisure is short. The ovotestis folicles are well separated in *M. engeli* and *M. tuberculata*, but are congested in *M. digitata*.

Melibe engeli can readily be distinguished from other members of the genus by its transparent body and form of the rhinophoral sheaths and cerata. Internally, *M. engeli* is distinct from its sister taxa *M. digitata* and *M. tuberculata* in having stomach plates that alternate in size. Based on the

subsequent phylogenetic analysis, other taxa in other lineages appear to have developed this apomorphic state independently.

Melibe leonina (Gould, 1852)

Chioraera leonina Gould, 1852:310. Gould, 1856: pl. 26, figs. 404a,b.

MATERIAL EXAMINED.— CASIZ 07161, one specimen, 0.9 km w. of Moss Landing, Monterey County, California, on *Macrocystis*, 7 October 1970, G. McDonald.

DISTRIBUTION.— Known from the Pacific Coast of North America from Kodiak Island, Alaska to Bahía de los Ángeles, México (Behrens 1991).

EXTERNAL MORPHOLOGY.— Most of the external anatomy of this species has been previously described (MacFarland 1966; Gosliner 1987). The body is smooth without any trace of tubercles or papillae on the notum, cerata or anterior margin of the wide foot. Rounded tubercles are present on the notum and cerata. The cerata and body appear to lack zooxanthellae. The gonopore lacks associated papillae.

DIGESTIVE SYSTEM.— The smooth interior of the oral hood connects with the slightly elevated, smooth mouth. The buccal mass is wide and muscular, devoid of jaws or radula. The esophagus is short and the salivary glands are compact. The posterior of the stomach lacks chitinous plates. A glandular pouch is present on either side of the dorsal surface of the stomach that expands into the digestive gland ducts. The digestive gland is diffuse and ramifies only within the cerata. A branch of the digestive gland originates from the right side of the stomach and ramifies into the more than half of the first anterior ceras on the right side. A large branch of the digestive gland originates from the stomach on the left side, proximal to the entrance of the esophagus into the stomach. Bifurcating immediately, a branch ramifies within most of the anteriormost ceras on the left. The remaining elongate branch spreads posteriorly as an undivided, tubular duct that branches to each of the posterior cerata and ramifies well within the remaining cerata.

CENTRAL NERVOUS SYSTEM.— Gosliner (1987) described the arrangement of the tuberculate ganglia. An elongate commisure joins the pedal ganglia. The paired buccal ganglia are well separated from each other and are smooth in texture.

REPRODUCTIVE SYSTEM.— The arrangement of the reproductive organs has been previously described and figured (MacFarland 1966, pl. 54, fig. 1; Gosliner 1987, fig. 2b). The 40–60 ovotestis bodies are arranged in congested somewhat compound clumps of 2–4 bodies.

NATURAL HISTORY.— Specimens of *Melibe leonina* are found frequently on the blades of the kelp *Macrocystis* spp. and less commonly on eel grass, *Zostera marina* where they feed upon crustaceans (Ajeska and Nybakken 1976; Gosliner 1987).

DISCUSSION.— Based on the subsequent phylogenetic analysis, *Melibe leonina* is the most basal member of the genus. Despite its basal position within the genus, *M. leonina* has numerous derived features: flattened cerata, elongate outer row of oral hood papillae, tuberculate ganglia, an elongate penis, somewhat compound ovotestis follicles that are congested, a difuse digestive gland and digestive gland branches that are ramified into the cerata.

Melibe liltvedi Gosliner, 1987

Melibe liltvedi Gosliner, 1987:402, figs. 1b, 3, 8e, 9d, 10d.

MATERIAL EXAMINED.— CASIZ 073951, three specimens, Llandudno, Atlantic coast of Cape Peninsula, Cape Province, South Africa, 30 m depth, 1 February 1983, W.R. Liltved.

Distribution.— Known from the Atlantic coast of the Cape Peninsula, South Africa (Gosliner, 1987).

External morphology.— Gosliner (1987) described the external anatomy of this species and details were confirmed from examination of material in this study. Papillae are absent from the anterior border of the foot. The cerata and body appear to lack zooxanthellae. The gonopore lacks associated papillae.

Digestive System.— The smooth interior of the oral hood connects with the slightly elevated, smooth mouth. The buccal mass is wide and muscular, devoid of jaws or radula. The esophagus is short and the salivary glands are compact. The posterior portion of the stomach possesses 5–6 chitinous plates that are triangular in shape and equal in size. They are arranged in a uniform distributional pattern. The digestive gland is a compact mass that is ramified around the stomach. A branch of the digestive gland originates from the right side of the stomach and ramifies into the more than half of the first anterior ceras on the right side. Another large branch of the digestive gland originates from the stomach on the left side, proximal to the entrance of the esophagus into the stomach. Bifurcating immediately, a branch ramifies within most of the anteriormost ceras on the left. The remaining elongate branch spreads posteriorly as an undivided, tubular duct that branches into each of the posterior cerata and ramifies well within the remaining cerata.

Central nervous system.— Gosliner (1987) described the arrangement of the smooth major ganglia. The pleural ganglia are well seperated from the cerebral ganglia. An elongate commissure joins the pedal ganglia. The paired buccal ganglia are adjacent to each other and are smooth in texture.

Reproductive system.— The arrangement of the reproductive organs has been previously described (Gosliner 1987, fig. 3d). The ovotestis forms a solid mass of compound bodies.

Discussion.— *Melibe liltvedi*, together with its sister species, *M. rosea*, forms a relatively basal clade within the genus. Both species in this clade share three synapomoprhies, the presence of a semi-serial receptaculum seminis, pleural ganglia that are well seperated from the cerebral ganglia and the buccal ganglia that are adjacent to each other. This latter feature has also developed independently in other lineages of *Melibe*. *Melibe liltvedi* differs in several regards from its sister species. The most obvious difference in distinguishing *M. liltvedi* from *M. rosea* is the coloration of the living animals. *Melibe liltvedi* is opaque white, whereas *M. rosea* is pink to orange in color. In *M. liltvedi*, the rhinophore sheath is ornamented with papillae, whereas in *M. rosea* they are absent. The inner surface of the oral hood is smooth in *M. liltvedi* and finely papillate in *M. rosea*. Internally, *M. liltvedi* lacks any remnant of jaws, whereas they are present in *M. rosea*. The bursa copulatrix of *M. liltvedi* is pyriform and spherical in *M. rosea*.

Melibe megaceras Gosliner, 1987

Melibe megaceras Gosliner, 1987:404, figs. 1c, 4, 5, 8g, 9f, 10e.

Material examined.— CASIZ 076164, one specimen, Coconut Island, Kaneohe Bay, Oahu, Hawaii, 3 July 1981, T.M. Gosliner. CASIZ 076165, one specimen, collected from sand bar, Kaneohe Bay, Oahu, Hawaii, 25 October 1986, T.M. Gosliner.

Distribution.— This species was previously known only from the Hawaiian Islands (Gosliner 1987). A photograph from Carole Harris and second from Burt Jones and Maurine Shimlock indicate that this species is also present from Dubai and Indonesia, respectively. Additional photographs from Malaysia are posted on the Sea Slug Forum (Rudman 2003). These additional records suggest that this species is widely distributed in the Indo-Pacific.

External morphology.— The external anatomy for this species was described by Gosliner (1987) and details were confirmed from material examined in this study. The body is covered with uniformly scattered, elongate papillae. The smooth, elongate cerata are inflated and have 2–4 elongate apical branches. The rhinophore sheaths have a single elongate papilla on the posterior surface. Papillae are absent from the anterior border of the wide foot. The oral hood is small and bears two rows of tentacles along the anterior margin. The outer row consists of uniformly small tentacles, while the inner row has tentacles of alternating large and small sizes. The cerata and body appear to contain zooxanthellae. The gonopore lacks associated papillae.

Digestive System.— The finely papillate interior of the oral hood connects with the slightly elevated, papillate mouth. The buccal mass is wide and muscular, devoid of jaws or radula.

There is a small, compact, globular salivary gland on either side of the buccal mass. The buccal mass connects to the short esophagus, which expands abruptly into the muscular, saccate stomach, which contains 20–24 thin triangular plates with eccentric apices in the posterior portion of the specimens dissected. The majority of the plates is nearly equal size, and is aligned in a regular fashion. Three to four smaller plates are found in some specimens, but these smaller plates do not alternate with the larger ones in a regular manner. The digestive gland is diffuse and surrounds the stomach. The two anterior branches of the digestive gland enter more than half of the two anteriormost cerata. The posterior digestive branch is not well developed and simply surrounds the stomach. No branches of the posterior digestive gland enter any of the posterior cerata.

Central nervous system.— The smooth cerebral and pleural ganglia are completely fused together. An elongate commissure joins the pedal ganglia. The paired, smooth, spherical buccal ganglia are adjacent to each other on the ventral portion of the esophagus. Darkly pigmented eyes are present on the dorsal surface of the cerebral ganglia.

Reproductive system.— The arrangement of the reproductive system is triaulic and was previously described by Gosliner (1987). Additional details are added here. The thirteen simple ovotestis follicles are congested. The preampullary duct enters the saccate ampulla, bifurcating distally into an oviduct and vas deferens. The vas deferens directly enters the spherical prostate, emerging as a thin tube within the penial sac, entering the base of the short, flat, spatulate penis. The oviduct widens slightly into a serial receptaculum seminis, then narrows slightly, proceeding distally towards the junction of the spherical bursa copulatrix and the duct of the female gland mass near the gonopore. The vagina contains a nodular gland near its distal opening.

Discussion.— The subsequent phylogenetic analysis indicates that *Melibe megaceras* is the sister species to a large clade containing seven Indo-Pacific taxa (Fig. 25). All members of this large clade share several synapomorphies. These eight taxa have papillae on the surface of the oral hood, papillae on the rhinophore sheaths (which have secondarily been lost in *M. viridis*), a papillate body surface (which has been secondarily modified in *M. digitata and M. tuberculata)* and the presence of a nodular vaginal gland that is either external or internal. *Melibe megaceras* can be most easily distinguished from the other members of this clade, as well as from other members of the genus, by its elongate cerata with 2–4 elongate branches, a posterior digestive gland branch that does not enter any of the cerata and a flattened paddle-shaped penis. *Melibe megaceras* is similar to *M. digitata* and *M. tuberculata* in that ceratal tubercles are absent.

Melibe minuta Gosliner and Smith, sp. nov.
(Figs. 1b, 10–12)

Type material.— Holotype: CASIZ 078529, one specimen, collected at 3 m depth, on live stony coral bottom, Horseshoe Cliffs, 1 km WNW of Onna Village, Okinawa, Ryukyu Islands,

Japan, 16 July 1991, R.F. Bolland. PARATYPES: CASIZ 078517, 10 specimens, collected at 3 m depth, on live stony coral bottom, Horseshoe Cliffs, 1 km WNW of Onna Village, Okinawa, Ryukyu Islands, Japan, 30 May 1991, R.F. Bolland. CASZ 078518, 22 specimens, collected at 3 m depth, on live stony coral bottom, Horseshoe Cliffs, 1 km WNW of Onna Village, Okinawa, Ryukyu Islands, Japan, 18 May 1991, R.F. Bolland. CASIZ 078519, 20 specimens, collected at 3 m depth, on live stony coral bottom, Horseshoe Cliffs, 1 km WNW of Onna Village, Okinawa, Ryukyu Islands, Japan, 18 May 1991, R F. Bolland. CASIZ 078521, five specimens, collected at 3 m depth, on live stony coral bottom, Horseshoe Cliffs, 1 km WNW of Onna Village, Okinawa, Ryukyu Islands, Japan, 19 May 1991, R.F. Bolland. CASIZ 078522, three specimens, collected at 3 m depth, on live stony coral bottom, Horseshoe Cliffs, 1 km WNW of Onna Village, Okinawa, Ryukyu Islands, Japan, 2 June 1991, R.F. Bolland. CASIZ 078533, four specimens, collected at 3 m depth, on live stony coral bottom, Horseshoe Cliffs, 1 km WNW of Onna Village, Okinawa, Ryukyu Islands, Japan, 9 June 1991, R.F. Bolland. CASIZ 086601, seven specimens, collected at 3 m depth, on live stony coral bottom, Horseshoe Cliffs, 1 km WNW of Onna Village, Okinawa, Ryukyu Islands, Japan, 9 March 1992, R.F. Bolland. CASIZ 087918, one specimen, collected at 1.5 m depth, on live stony coral bottom, Horseshoe Cliffs, 1 km WNW of Onna Village, Okinawa, Ryukyu Islands, Japan, 13 July 1992, R.F. Bolland.

DISTRIBUTION.— Locally common, but so far limited only to the Horseshoe Cliffs area of the Ryukyu Islands in Okinawa.

ETYMOLOGY.— This species is named *minuta* owing to the small size of the adult specimens.

EXTERNAL MORPHOLOGY.— The living animals are translucent and are brownish green in color (Fig. 1b). The preserved specimens range in size from 3–10 mm in length and are firm and fleshy (Fig. 10a). The general body shape is limaciform, somewhat elongated, and not compressed anterolaterally. Posterior to the oral hood, the body is humped and rounded in the cardiac and visceral region, tapering abruptly into the posterior portion of the foot, which is often tapered and curled. Ventral to the visceral and cardiac area the rounded body flattens somewhat to form the sides of the foot. The body surface is mostly smooth, with some rugose areas around the neck, cerata bases, and the side of the foot. There may be some low tubercles on the dorsal portion of the neck, and some small opaque, apparently glandular spots or tiny tubercles in the area dorsal to the foot margin. The foot has a narrow, entire, anterior margin, which is rounded in ventral view (Fig. 10b). There are no associated foot papillae. The foot becomes wider near the middle of the body, with a clearly defined sole and foot margin visible when viewed from above. The foot tapers posteriorly and projects behind the body proper. Posterior to the projecting, entire, anterior portion, the foot margin becomes undulate. The oral hood is produced from a narrowed base, which lies posterior to the projecting anterior foot margin. The hood is small relative to the body, and its entire, circular margin typically bears an inner and an outer row of cylindrical papillae with rounded or bulbous apices (Fig. 10b). The outer row is significantly longer and larger, and the inner row may be so short in places that it could be described as a series of tubercles. In some specimens additional rows or partial rows of papillae are present, usually in the anterior portion, to a maximum of 4 rows. The hood surface tends to be more translucent than the margin, and in some specimens is covered with fine white glandular dots, which appeared as low rounded tubercles in others. There are no accessory papillae on the hood surface. The widely seperated rhinophoral sheaths arise from the hood surface just anterior to the neck (Figs. 10a,e). In general, they are cylindrical and simple, with no sail or large projections, widening and thickening at the distal portion to produce a flanged margin that may be entire and simple, or ornamented with bead-like projections, or short crenulations with rounded apices. In detail, the form varies between an elongate cylinder that widens gradually at the apex to a distinct, shorter, somewhat annulate basal portion with a seperately defined distal

cup or calyx. The rhinophores are perfoliate with three or four lamellae (Fig 10e). There are 4–6 cerata on each side of the dorsum, the anteriormost being opposite in arrangement, becoming more alternate posteriorly (Fig 10a). The fleshy cerata arise from a cylindrical base and spread and flatten into fan shaped, oval, or spatulate distal portions which tend to become concave on the inner surfaces, the margins thickened and inrolled. The margins bear a complex combination of multifid projections and papillations, single papillae, crenulations, and tubercles. The convex inner surfaces bear similar protuberences, while the outer surfaces range from bearing low glandular opaque spots to circular raised tubercles creating a nodular appearance (Figs.10c–d). While the cerata of the living animals may be somewhat translucent, it is not possible to externally ascertain the presence of branches of the digestive gland within them. In the preserved specimens the cerata are firmly held nearly vertical or in a "V". It appears that autotomy or dehiscence is less apt to occur in this species as there are few detached cerata present. The anus is located on a distinctly raised papilla located anterodorsal to the second anterior ceras on the right side. The nephroproct is immediately dorsal to the anus. The gonopore is anteroventral to the most anterior right ceras. There are no papillae associated with the gonopore. In many of the specimens a subdermal black eyespot is observable on the left side below the anteriormost ceras. The right eyespot is most often hidden by the genital organs.

Digestive System.— The finely papillate oral hood interior leads to the papillate mouth. The oral tube does not significantly expand into the buccal mass, which is narrow, lacks musculature, and is devoid of any vestiges of jaws or radula. There is a small, compact, globular salivary gland on either side of the buccal mass. The buccal mass is continuous with the elongate esophagus, which expands abruptly into the muscular, saccate stomach, which contained 8 or 9 thin triangular plates in the posterior portion of the specimen dissected (Figs. 12a–c). The plates are of near equal size, and are aligned in a regular fashion. The arrangement of the digestive gland is much the same as described for *Melibe tuberculata*.

Central nervous system.— The smooth cerebral and pleural ganglia are fused (Fig. 11b). An elongate commissure joins the pedal ganglia together. Each of a pair of spherical buccal ganglia is touching side by side on the ventral portion of the esophagus. Darkly pigmented eyes are present on the dorsal surface of the cerebral ganglia.

Reproductive system.— The arrangement of the reproductive system is triaulic (Fig. 11a). The five simple ovotestis follicles are congested. The preampullary duct enters the saccate ampulla, bifurcating distally into an oviduct and vas deferens. The vas deferens directly enters the spherical prostate, emerging as a thin tube within the penial sac, entering the base of the short, conical penis. The oviduct widens slightly into a serial receptaculum seminis, then narrows slightly, proceeding distally towards the junction of the pyriform bursa copulatrix and duct of the female gland mass near the gonopore. A vaginal gland is not present.

Natural history.— This species has been found at depths between 1.5 and 4 meters, on or within chunks of living and dead hermatypic coral with growths of *Acanthophora* sp. (R.F. Bolland, pers. commun.)

Discussion.— *Melibe minuta* is the most basal member of the tropical Indo-Pacific clade of *Melibe* species. All of these species are unique in possessing brownish coloration that is most likely indicative of the presence of zooxanthellae. Most members of this clade have a papillate body surface (except for *M. digitata* and *M. tuberculata* where they have been secondarily lost) and papillae on the cerata (with the exception of *M. megaceras* where they have been secondarily lost). *Melibe minuta* is easily recognizable externally by its small body size and the flattened cerata with an inrolled margin. The outer row of papillae on the oral hood is the longest.

***Melibe papillosa* (de Filippi, 1867)**
(Figs. 13, 14)

Jacunia papillosa de Filippi, 1867:233–234.
Melibe papillosa (de Filippi, 1867).
Melibe fimbriata Debelius, 1996, misidentification: 288, upper photo.

MATERIAL EXAMINED.— CASIZ 076181, one specimen, intertidal zone, Choshaga Saki, Sagami Bay, Honshu, Japan, 21 June 1970, F. Steiner. CASIZ 089005, one specimen, 41 m depth, Seragaki Beach, 1.3 km ene of Maekizaki, Okinawa, Ryukyu Islands, Japan, 29 November, 1992, R.F. Bolland. CASIZ 075960, one specimen, 2 m depth, Seragaki Beach, 1.3 km ene of Maekizaki, Okinawa, Ryukyu Islands, Japan, 20 July, 1991, R.F. Bolland.

DISTRIBUTION.— Known from the Japan (De Filippi 1867; Baba 1949), Okinawa (present study) and Indonesia (Debelius 1996).

EXTERNAL MORPHOLOGY.— The living animals as seen in photos not published in the present study have a golden brown ground color, with brown and opaque white blotches present on notum and cerata, along with dispersed patterns of tiny white flecks or glandular dots. The animal is translucent to transparent, and portions of internal organs and the substratum can be seen through the body. The preserved specimens reach a maximum length of 50 mm. The body is elongate, limaciform, and somewhat compressed anterolaterally, with a dorsally elevated hump in the cardiac region and tapering gradually to a slender posterior portion of the foot. Thin, elongate papillae are present on the notum and cerata. The opaque, narrow, linear foot has a rounded, entire, anterior margin becoming somewhat undulate on the lateral portions. There are no papillae proximal to the anterior portion of the foot. The large oral hood has a circular, entire margin with two rows of cylindrical papillae, which taper to conical points, with the innermost row being the longer. There are scattered papillae on the surface of the oral hood. The well-separated, perfoliate rhinophores (Fig.13a) have 12 lamellae and arise from the surface of the oral hood within cylindrical sheaths that have a narrow posterior sail with a simple elongate dorsal projection. The three to six pairs of cerata (Fig.13b) are apically flattened with a regular wedge shaped margin, bearing a few thin papillae along the margin. The anus is located immediately anterior to the second ceras on the right side of the body. The nephroproct is immediately dorsal to the anus. The gonopore is on the right side of the body below and slightly anterior to the first ceras and bears a circle of papillae around the genital aperture.

DIGESTIVE SYSTEM.— The finely papillate interior of the oral hood connects with the slightly elevated, papillate mouth (Fig. 13c). The buccal mass is wide and muscular, devoid of a radula, but containing a pair of thin, chitinous jaws with a denticulate masticatory border (Fig. 14a). A pair of elongate nodular salivary glands lies on either side of the middle portion of the buccal mass. The short, wide esophagus emerges from the posterior of the buccal mass and expands into the saccate, muscular stomach. The posterior of the stomach contained 23 triangular, chitinous plates, with thickened, eccentric apices arranged in an alternating manner (Fig. 14b). The plates also alternate between large and small in size. The intestine leaves the posterodorsal stomach and curves dorsally, straightening and ending at the anus. A branch of the diffuse digestive gland originates from the right side of the stomach and ramifies into more than half of the first anterior ceras on the right side. A large branch of the digestive gland originates from the posterolateral stomach on the left side, proximal to the entrance of the esophagus into the stomach. Bifurcating immediately, a branch ramifies into more than half of the anteriormost ceras on the left. The remaining elongate branch spreads posteriorly, interdigitating with the ovotestis and ramifying into more than half of the next pair of posterior cerata, after which it continues to ramify posteriorly, but does not enter into any of the remaining cerata.

CENTRAL NERVOUS SYSTEM.— The cerebral, pleural and pedal ganglia are largely separate but are situated in close proximity to each other (Fig. 13c). All these ganglia have a granular appearance caused by the presence of distinct, peripheral, globular nerve cells. An elongate commisure joins the pedal ganglia. The paired buccal ganglia lie adjacent to each other on the ventral surface of the esophagus, and are connected to the cerebral ganglia by paired nerves. Each buccal ganglion is smooth with an additional outlying esophageal ganglion lateral to each buccal ganglion.

REPRODUCTIVE SYSTEM.— The dissected specimen has more than 50 compound, spherical, congested ovotestis bodies. The ovotestis bodies are arranged in compound clumps of two bodies. The narrow preampullary duct widens slightly and enters the highly convoluted ampulla posteriorly (Fig. 13d). The ampulla constricts at the distal portion that branches into the oviduct and vas deferens. The slender vas deferens is elongate and straight. It then enters into the spherical, lobate prostate before exiting, enlarging, and making several bends before penetrating the bulbous proximal end of the conical penis, which lies within the penial sac. The distal end of the penial papilla is slightly curved. The penial sac terminates proximally to the gonopore. The large, smooth mucous gland comprises most of the female gland mass, along with the nodular albumen gland and folded membrane gland. The proximal oviduct is undulate and widens into a distinct portion that probably serves as a serial receptaculum seminis. The oviduct recurves and narrows and enters the basal portion of the vagina. The proximal portion of the elongate vagina connects with the large, pyriform bursa copulatrix. A distinct banded vaginal gland is present internally around the vagina.

DISCUSSION.— This species has been the subject of considerable confusion. Several workers have considered *M. papillosa* (de Filippi, 1867) and *M. vexillifera* Bergh, 1880 as synonyms of *M. pilosa* (Pease, 1860) (Eliot 1907; Odhner 1936; Edmunds and Thompson 1972; Gosliner 1987). However, after re-examination of specimens of these taxa in this study, it is evident that the three taxa are closely related, but distinct from each other. *Melibe papillosa* is the sister species to the clade containing *M. viridis* (*M. vexillifera* appears to be a synonym of this species) and *M. bucephala*. Members of this clade have buccal ganglia that are adjacent to each other and stomach plates that alternate in size. *Melibe papillosa* differs from these other two species in having two rows of papillae on the oral hood while *M. bucephala* and *M. viridis* have 3–5 and 2–5 rows, respectively. In *M. papillosa*, the posterior digestive gland enters only the first post cardiac cerata while in *M. bucephala* and *M. viridis* the digestive gland enters the first two ceratal rows.

In its general body form *Melibe papillosa* most closely resembles *M. pilosa*. This resemblance has created confusion in their taxonomic distinction. Following examination of specimens of these two taxa in the present study, several consistent anatomical differences were confirmed. The jaws of *M. pilosa* have a smooth masticatory, border while those of *M. papillosa* are denticulate. *Melibe pilosa* has stomach plates that are all relatively large while in *M. papillosa* they are alternating in size and alignment. In *M. papillosa*, the branches of the posterior digestive gland entering only the first posterior cerata while in *M. pilosa* they enter the first two of the posterior cerata. In *M. papillosa* the buccal ganglia are adjacent to each other, while in *M. pilosa* they are in contact with each other.

Melibe pilosa Pease, 1860
(Figs.15–17)

Melibe pilosa Pease, 1860:34. O'Donoghue, 1929:803, fig. 220.

MATERIAL EXAMINED.— CASIZ 061506, intertidal to 1 m depth, Diamond Head Beach Park, Oahu, Hawaiian Islands, 8 February 1986, M.T. Ghiselin. CASIZ 061501, 2 m depth, Sand Island, Kaneohe Bay, Oahu, Hawaiian Islands, 10 February 1986, T.M. Gosliner. CASIZ 016677, shallow

water, Waikiki Beach, Oahu, Hawaiian Islands, 11 March 1939, D.P. Abbott. CASIZ 087402, Easter Island, L. De Salvo.

Distribution.— Known from the Hawaiian Islands (Pease 1860; Gosliner 1987) and Easter Island (present study).

External morphology.— The translucent living animals as seen in photographs not shown in the present study have a grayish brown ground color, with brown and opaque white blotches present on notum and cerata, along with dispersed patterns of tiny brown spots. The preserved specimens reach a maximum length of 80 mm. The body is elongate, limaciform, and somewhat compressed anterolaterally, with a dorsally elevated hump in the cardiac region and tapering gradually to a slender posterior portion of the foot. Thin, elongate papillae are present on the notum and cerata. The opaque, narrow, linear foot has a rounded, entire, anterior margin becoming somewhat undulate on the lateral portions. There are no papillae proximal to the anterior portion of the foot. The large oral hood has a circular, entire margin with three rows of cylindrical papillae, which taper to conical points, with the innermost row much longer and thicker than the outer ones. There are scattered papillae on the surface of the oral hood. The well-separated, perfoliate rhinophores (Fig. 15b) have 10 lamellae and arise from the surface of the oral hood within cylindrical sheaths that have a narrow posterior sail with a simple elongate dorsal projection. There are four to nine pairs of cerata (Fig. 15a) which are apically flattened with a regular wedge shaped margin, bearing a few thin papillae along the margin. The anus is located immediately anterior to the second ceras on the right side of the body. The nephroproct is immediately dorsal to the anus. The gonopore is on the right side of the body below and slightly anterior to the first ceras and bears a circle of papillae around the genital aperture.

Digestive System.— The finely papillate interior of the oral hood connects with the slightly elevated, papillate mouth. The buccal mass (Fig. 16b) is wide and muscular, devoid of a radula, but containing a pair of thin, chitinous jaws with a smooth masticatory border (Fig. 17a). A pair of elongate nodular salivary glands lies on either side of the middle portion of the buccal mass. The short, wide esophagus emerges from the posterior of the buccal mass and expands into the saccate, muscular stomach. The posterior of the stomach contained 17 triangular, chitinous plates, with thickened, eccentric apices arranged uniformly (Figs. 17b–c). The plates are subequal in size, but do not alternate between large and small plates. The intestine leaves the posterodorsal stomach and curves dorsally, straightening and ending at the anus. A branch of the diffuse digestive gland originates from the right side of the stomach and ramifies into more than half of the first anterior ceras on the right side. A large branch of the digestive gland originates from the posterolateral stomach on the left side, proximal to the entrance of the esophagus into the stomach. This branch ramifies around the stomach. Bifurcating immediately, another branch ramifies into more than half of the anteriormost ceras on the left. The remaining elongate branch spreads posteriorly, interdigitating with the ovotestis and ramifying into more than half of the next two pairs of posterior cerata, after which it continues to ramify posteriorly, but does not enter into any of the remaining cerata.

Central nervous system.— The cerebral, pleural and pedal ganglia are largely separate but are situated in close proximity to each other (Fig. 16b). All these ganglia have a granular appearance caused by the presence of distinct, peripheral, globular nerve cells. An elongate commisure joins the pedal ganglia. The paired buccal ganglia are in contact with each other on the ventral surface of the esophagus, and are connected to the cerebral ganglia by paired nerves. Each buccal ganglion is smooth with an additional outlying esophageal ganglion lateral to each buccal ganglion.

Reproductive system.— The dissected specimen has more than 20 compound, spherical, congested ovotestis bodies. The ovotestis bodies are arranged in compound clumps of 2–3 bodies. The narrow preampullary duct widens slightly and enters the highly convoluted ampulla posterior-

ly (Fig. 16a). The ampulla constricts at the distal portion that branches into the oviduct and vas deferens. The slender vas deferens is elongate and straight. It then enters into the spherical, lobate prostate before exiting, enlarging, and making several bends before penetrating the bulbous proximal end of the conical penis, which lies within the penial sac. The distal end of the penial papilla is slightly curved. The penial sac terminates proximally at the gonopore. The large, smooth mucous gland comprises most of the female gland mass, along with the nodular albumen gland and folded membrane gland. The proximal oviduct is undulate and widens into a distinct portion that probably serves as a serial receptaculum seminis. The oviduct recurves and narrows and enters the basal portion of the vagina. The proximal portion of the elongate vagina connects with the large, pyriform bursa copulatrix. A distinct banded vaginal gland is present internally around the vagina.

Natural history.— *Melibe pilosa* is found relatively commonly in shallow waters of 0.5–10 meters depth. Generally it is found in association with a variety of marine algae including *Padina* sp. and *Acanthophora* sp.

Discussion.— As discussed previously under the discussion of *M. papillosa*, *M. pilosa* has been the subject of considerable taxonomic confusion. It is clearly distinct from *M. papillosa* and *M. viridis*. *Melibe pilosa* is the sister taxon to the clade containing *M. papillosa* (de Filippi 1867), *M. bucephala* Bergh, 1902 and *M. viridis* Kelaart, 1858. Members of this clade share several apomorphies. They share several external features including a large oral hood, flattened cerata, a circle of papillae surrounding the genital aperture, and an oral hood with two or more rows of papillae. Their central nervous system has tuberculate ganglia with well-separated cerebral and pleural ganglia. The digestive system contains elongate salivary glands and the digestive gland ducts enter only the first one or two cerata of the posterior digestive branch. All four species have an internal vaginal gland.

Melibe pilosa and *M. viridis* differ from *M. papillosa* and *M. bucephala* in having a smooth rather than denticulate masticatory margin of the jaws. *Melibe pilosa* has fewer stomach plates (16–17) than the other members of this clade, which have more than 20 plates. In *M. pilosa* the plates are arranged uniformly, while in the three species that comprise the sister taxon have plates whose apices alternate in their arrangment.

Melibe rosea Rang, 1829

(Figs. 18a, b)

See Gosliner (1987) for synonymy and references.

Material examined.— CASIZ 061503, two specimens, dissected, Algoa Bay, Cape Province, South Africa, 10 m depth, 14 May 1984, W.R. Liltved. SAM A33980, four specimens, dissected, Dale Brook, False Bay, Cape Province, South Africa, on the underside of intertidal rocks, 18 November 1979, T.M. Gosliner.

Distribution.— This species is known only from the temperate waters of southern Africa from Port Nolloth on the Atlantic coast to Port Alfred in the Indian Ocean (Gosliner 1987).

External morphology.— Gosliner (1987) described the external anatomy for this species and details were confirmed from material examined in this study. The oral hood is large and devoid of small papillae over its surface. It has two or three rows of papillae along the anterior margin that are more or less equal in length. The cerata are inflated and bear numerous rounded tubercles. Papillae are absent from the anterior border of the foot. The cerata and body lack zooxanthellae. The well- separated rhinophore sheaths are simple, without papillae or appendages. The gonopore lacks associated papillae.

Digestive System.— The finely papillate interior of the oral hood connects with the slightly elevated, smooth mouth. The buccal mass is wide and muscular, and contains a pair of chitinous jaws (Fig.18a). The jaws have 14–22 rounded denticles along either masticatory margin. The esophagus is short and the salivary glands are compact. The posterior of the stomach possesses 7–8 chitinous plates that are symmetrically triangular in shape and equal in size (Fig. 18b). They are arranged in a uniform distributional pattern. The digestive gland is a compact mass that is ramified around the stomach. A branch of the digestive gland originates from the right side of the stomach and ramifies into more than half of the first anterior ceras on the right side. A large branch of the digestive gland originates from the stomach on the left side, proximal to the entrance of the esophagus into the stomach. Bifurcating immediately, a branch ramifies within most of the anteriormost ceras on the left. The remaining elongate branch spreads posteriorly as an undivided, tubular duct that branches to each of the posterior cerata and ramifies well within the remaining cerata.

Central nervous system.— The arrangement of the smooth major ganglia was described by Gosliner (1987). The pleural ganglia are well separated from the cerebral ganglia. An elongate commisure joins the pedal ganglia. The paired buccal ganglia are adjacent to each other and are smooth in texture.

Reproductive system.— The arrangement of the reproductive organs has been previously described (Gosliner 1987, fig. 3d). The ovotestis forms a solid mass of compound bodies.

Discussion.— As mentioned under the discussion of *M. liltvedi*, *M. rosea* is the likely sister species of *M. liltvedi*. Both species have a semi-serial receptaculum seminis and buccal ganglia that are adjacent to each other. In addition to the external differences noted above, *Melibe rosea* has denticulate jaws while *M. liltvedi* lacks any vestige of jaws. *Melibe rosea* has a spherical bursa copulatrix while the bursa is pyriform in *M. liltvedi*.

Melibe tuberculata Gosliner and Smith, sp. nov.

(Figs. 1c, 19–21)

Type Material.— Holotype: California Academy of Sciences, CASIZ 105639, one specimen, collected at 1.5 m depth, Bonito Island, Maricaban Island, Batangas Province, Luzon, Philippines, 27 February, 1995, T.M. Gosliner. Paratype: CASIZ 106394, one specimen dissected, collected at 8 m depth, Devil's Point, Maricaban Island, Batangas Province, Luzon, Philippines, 15 April, 1996, T.M. Gosliner.

Distribution.— This species has thus far been reported only from the Batangas Province of the Luzon Island in the Philippines.

Etymology.— The name *tuberculata* refers to the rounded tubercles covering the surface of the cerata.

External morphology.— The living animal (Fig. 1c) has a translucent, brownish green body, with the cerata possessing a more vivid, opaque green appearance. The preserved specimens are 11 mm and 15 mm in length. The body is limaciform, somewhat compressed anterolaterally, humped over the visceral region, tapering posteriorly to a rounded posterior portion of the foot (Fig. 19a). The preserved body is pale yellow-white in color and is semi-transparent, with the organs and a criss-crossing network of muscle fibers visible through the body wall. The texture of the dorsum is essentially smooth, with very fine opaque glandular spots or tubercles scattered throughout, but more concentrated near the margin of the foot. The foot is narrow and linear, with an opaque margin that is somewhat undulate along its length, and an anterior margin that is entire and rounded. There are 2 small papillae on or proximal to each side of the anterior margin of the foot. The oral hood is quite small compared to the body, and has an entire, circular margin

(Fig.19a). An inner and an outer row of papillae are present, which are more or less equal in length, with the anteriormost appearing slightly longer. The papillae are cylindrical, with the inner row tapering to acute apices, while the outer row tends to be less tapered and more rounded apically.

The dorsal surface of the hood bears larger club shaped or bulbous papillae, arranged in two rows with the most basal row being the largest. Small white glandular dots or tubercles are present on the translucent surface of the hood, while the hood margin appears more opaque. The well-separated rhinophoral sheaths arise just posterior to the slightly constricted neck separating body from hood. The sheaths are elongate and cylindrical, widening at the distal margin into a corona of 6–12 anterior tubercles and a single posterior elongate papilla (Fig. 19c). The smooth arborescent cerata arise from cylindrical bases into trunks extending approximately 1/4th of the total length before producing multiple branches which terminate in elongate, bulbous, rounded papillae (Fig. 19b). The cerata are dehiscent along their base, and appear to be shed or autotomized easily, as most are no longer attached. There appear to be 4–5 cerata per side, arranged close to the midline. The anus is located on a low elevation located just anterior to the second anterior ceras on the right side, slightly dorsal to the ceratal midline. The nephroproct is immediately dorsal to the anus, on the anal papillae. The gonophore is directly ventral to the anteriormost right ceras, proximal to the lateral midline. There are no papillae associated with the gonopore. One specimen was observed to have a single slightly lobed papilla on an elevated base located medially, proximal to the midline of the dorsum. The second specimen had a much smaller papilla without the elevated base located just anterior to the posteriormost left ceras (Fig. 19a).

Digestive system.— The finely papillate inner surface of the oral hood leads to a mouth with a papillate surface. A wide muscular buccal mass leads to an elongate esophagus, which widens into a saccate muscular stomach. A pair of compact salivary glands lies one on each side of the muscular portion of the buccal mass. A radula is entirely lacking, but a pair of chitinous jaws with smooth masticatory surfaces was present in the muscular fold of the buccal mass (Fig. 21a). The posterior portion of the stomach contained 16 chitinous plates of subequal size, with alternately arranged eccentric apices (Figs. 21b–c). The wide intestine emerges from the dorsal stomach, narrowing as it curves anteriorly, recurving posteriorly before reaching the anus. The diffuse digestive gland originates ventrolaterally on the left side of the stomach. A thin branch proceeds anterodorsally, crossing over the esophagus and entering the first ceras on the right side, where it ramifies into less than half the length of the ceras. A second slightly wider branch proceeds dorsally to enter and ramify into the first ceras on the left side. A larger branch of the digestive gland proceeds posteriorly, entering and ramifying into the remaining cerata.

Nervous system.— All of the ganglia are smooth in texture, with the pleural ganglia well separated (Fig. 20b). The pedal ganglia are joined by a short pedal commisure. The smooth spherical buccal ganglia are situated on the ventral esophagus in such a way that they are touching each other. Each of a pair of dark eye-spots are located on either lobe of the cerebral ganglia.

Reproductive system.— The arrangement of the reproductive system (Fig. 20a) is triaulic. There are four simple, well-separated ovotestis follicles. The preampullary duct enters the proximal lobe of the expanded ampulla, with the distal lobe bifurcating into a tubular vas deferens, and an oviduct. The vas deferens proceeds in a linear manner for a distance equal to the length of the ampulla before recurving and entering the spherical prostate. Emerging from the prostate, the thinner distal portion undergoes several convolutions before entering the proximal portion of the conical penis, the distal end of which lies near the gonopore. After emerging from the ampulla, the oviduct immediately enters a serial, expanded receptaculum seminis, which then narrows, making two convolutions before joining with the female atrium distal to the nodular vaginal gland, where it is joined by the elongate duct from the spherical bursa copulatrix. The female gland mass is also

connected to the atrium, and consists of a larger, smooth, mucous gland, a smaller, folded membrane gland, and a nodular albumen gland.

NATURAL HISTORY.— This species has been found in shallow water underneath rocks, and in both occurrences it was found under the same rock as specimens of *Melibe digitata*.

DISCUSSION.— *Melibe tuberculata* appears to be the sister species of *M. digitata* and the synapomorphies shared by these taxa are described in the discussion of *M. digitata*. Differences between the two taxa are also noted in this discussion.

Melibe viridis (Kelaart, 1858)

(Figs. 22, 23)

Meliboea viridis Kelaart, 1858:113.
Melibe fimbriata Alder and Hancock, 1864:138, pl. 33, figs. 6–7.
Melibe vexillifera Bergh, 1880:162, pl. 2, figs. 1–11, pl. 3. figs. 1–3.
Propomelibe mirifica Allan, 1932:314, pl. 24, figs. 1–8.

MATERIAL EXAMINED.— CASIZ 103727, two specimens, 8 m depth, Seafari Beach, Balayan Bay, Batangas Province, Luzon Island, Philippines, 24 February, 1995, L. Losito. CASIZ 083671, three specimens, 5 m depth, Seafari Beach, Balayan Bay, Batangas Province, Luzon Island, Philippines, 17 February, 1992, T.M. Gosliner. CASIZ 061505, Inhaca Island, Mozambique, 1 July 1955, W. Macnae. CASIZ 078516, one specimen, 64 m depth, Seragaki Beach, 1.3 km ene of Maekizaki, Okinawa, Ryukyu Islands, Japan, 20 July, 1991, R.F. Bolland.

DISTRIBUTION.— Known from the Indian and western Pacific Oceans from Mozambique (Macnae and Kalk 1958), Zanzibar (Eliot 1902, 1907), Sri Lanka (Kelaart 1858), India (Alder and Hancock 1864), Vietnam (Dawydoff 1952; Risbec 1956), Japan (Bergh 1880; Baba 1949), Okinawa (present study); Philippines (present study) and Australia (Allan 1932; Coleman 1989; Wells and Bryce 1993). This species has also been found in the Mediterranean Sea from Greece and has probably migrated there through the Suez Canal (Thompson and Crampton 1984).

EXTERNAL MORPHOLOGY.— The living animal as seen on a photo slide not shown in the present study has a tan ground color, with brown blotches present on notum and cerata, along with dispersed patterns of tiny white flecks or glandular dots. The animal is translucent to transparent, and portions of internal organs and the substrate can be seen through the body. The preserved specimens reach a maximum length of 130 mm. The body is elongate, limaciform, and somewhat compressed anterolaterally, with a dorsally elevated hump in the cardiac region and tapering gradually to a slender posterior portion of the foot. Rounded tubercles are present on the notum and cerata. The opaque, narrow, linear foot has a rounded, entire, anterior margin becoming somewhat undulate on the lateral portions. There are no papillae proximal to the anterior portion of the foot. The large oral hood has a circular, entire margin that produces two to five rows of cylindrical papillae, which taper to conical points, with the innermost row being the longest. There are scattered papillae or tubercles on the surface of the oral hood. The well-separated perfoliate rhinophores have 5 to 7 lamellae and arise from the surface of the oral hood within cylindrical sheaths bearing low tubercles. A posterior sail is absent from the rhinophore sheath, but a simple papilla is commonly present on the posterior side of the sheath of most of the animals examined. The five to nine cerata are somewhat flattened, saccate, oval to cylindrical with tubercular and papillate surfaces whose dark blotches persist in preservation (Fig.22c). They are arranged in two rows on either side of the dorsum, the anteriormost opposite, with the remainder alternate and increasingly offset toward the posterior. The anus is located immediately anterior to the second ceras on the right side of the body. The nephroproct is immediately dorsal to the anus. The gonopore is on the right side of the body

below and slightly anterior to the first ceras. A ring of papillae is associated with the gonopore.

Digestive System.— The coarsely papillate interior of the oral hood connects with the slightly elevated, papillate mouth. The buccal mass is wide and muscular, devoid of a radula, but containing a pair of thick, chitinous jaws with a smooth masticatory border (Fig. 22a). A pair of elongate nodular salivary glands lies on either side of the middle portion of the buccal mass. The short, wide esophagus emerges from the posterior of the buccal mass and expands into the saccate, muscular stomach. The posterior of the stomach contained 23 triangular, chitinous plates, with thickened, eccentric apices arranged in an alternating manner (Fig. 22b). The plates also alternate between large and small in size. The intestine leaves the posterodorsal stomach and curves dorsally, straightening and ending at the anus. A branch of the diffuse digestive gland originates from the right side of the stomach and ramifies into the basal portion of the first anterior ceras on the right side. A large branch of the digestive gland originates from the posterolateral stomach on the left side, proximal to the entrance of the esophagus into the stomach. Bifurcating immediately, a branch ramifies into the basal portion of the anteriormost ceras on the left. The remaining elongate branch spreads posteriorly, interdigitating with the ovotestis and ramifying into the basal portions of the next two pairs of posterior cerata, after which it continues to ramify posteriorly, but does not enter into any of the remaining cerata.

Central nervous system.— The cerebral, pleural and pedal ganglia are largely separate but are situated in close proximity to each other. All these ganglia have a granular appearance caused by the presence of distinct, peripheral, globular nerve cells. An elongate commisure joins the pedal ganglia. The paired buccal ganglia (Fig. 23b) lie adjacent to each other on the ventral surface of the esophagus, and are connected to the pedal ganglia by paired nerves. Each buccal ganglion consists of four or five well-fused cells, with an additional distinct esophageal ganglion lateral to each buccal ganglion.

Reproductive system.— The dissected specimen has more than 50 compound, spherical, congested ovotestis bodies. The ovotestis bodies are arranged in compound clumps of 2–4 bodies. The narrow preampullary duct widens slightly and enters the highly convoluted ampulla posteriorly (Fig. 23a). The ampulla constricts at the distal portion that branches into the oviduct and vas deferens. The slender vas deferens is elongate and straight. It then enters into the spherical, lobate prostate before exiting, enlarging, and making several bends before penetrating the bulbous proximal end of the conical penis, which lies within the penial sac. The distal end of the penial papilla is slightly curved. The penial sac terminates proximally to the gonopore. The large, smooth mucous gland comprises most of the female gland mass, along with the nodular albumen gland and folded membrane gland. The proximal oviduct is undulate and widens into a distinct portion that probably serves as a serial receptaculum seminis. The oviduct recurves and narrows and enters the basal portion of the vagina. The proximal portion of the elongate vagina connects with the large, pyriform bursa copulatrix. A distinct banded vaginal gland is present internally around the vagina.

Natural history.— These animals appear to be feeding on crustaceans, which they are able to ingest intact. The stomach of the 13 cm specimen from Mozambique contained the carapace of a crab, 13 mm across, nearly completely intact. The stomach contents of the 11 cm specimen from the Philippines included several intact ostracods, each approximately one mm in length, and a hermit crab in a snail shell two mm in height. In the field in the Philippines, specimens have been observed to feed on mysid shrimp at night. However, the mysids were attracted to a diver's underwater light and this may simply be an opportunistic feeding event rather than one that occurs under natural light conditions.

Discussion.— As noted above, in the discussion of *M. papillosa*, there has been much confusion surrounding the Indo-Pacific species of *Melibe* that have flattened cerata. In addition to *M.*

papillosa and *M. pilosa*, several names have been used to describe Indo-Pacific species with these kinds of cerata. The earliest name available is *Meliboea viridis* Kelaart, 1858, described from Sri Lanka (as Ceylon). Subsequent authors have largely ignored this species. The next most recent name is *Melibe fimbriata* Alder and Hancock, 1864, from India. Bergh (1880) described *Melibe vexillifera* from Japan. Most recently, Allan (1932) described *Propenelibe mirifica* from northern Queensland, Australia. Several workers considered *M. vexillifera* to be a synonym of M. *pilosa*, but have regarded *M. fimbriata* as a distinct species (Eliot 1907; Odhner 1936; Edmunds and Thompson 1972; Gosliner 1987).

Edmunds and Thompson (1972) suggested *that M. fimbriata* differs from *M. pilosa* and in several regards. They stated that in *M. pilosa* a distinct papilla is present on the posterior end of the rhinophore sheath but this is absent in *M. fimbriata*. However, Thompson and Crampton (1984) indicated that a papilla is present in Mediterranean specimens of *M. fimbriata*. The present study indicates that a small papilla is usually present in *M. fimbriata*. In *M. pilosa* and *M. papillosa* a posterior expansion of the rhinophore sheath forming a sail is present, while in *M. fimbriata* it is absent. Edmunds and Thompson stated that the pharynx and esophagus of *M. pilosa* are slightly longer than in *M. fimbriata*. However, examination of specimens of *M. papillosa*, *M. pilosa* and *M. viridis* in the present study, indicates that there is no significant difference in the length of these portions of the digestive tract in these three species. Edmunds and Thompson (1972) suggested that in *M. pilosa* a jaw is usually present while in *M. fimbriata*, it is generally absent. The specimen that they identified as *M. pilosa* from Tanzania had a pair of jaws, but it is unclear whether the masticatory margin was smooth or denticulate. Alder and Hancock (1864) did not describe specifically whether jaws were present or absent in their specimen of *M. fimbriata*, but indicated that jaws were typically absent in species of *Melibe*. Eliot (1902) recorded *M. fimbriata* from Tanzania and indicated that jaws were absent in the specimen he examined. Later, he (Eliot, 1907) re-examined the specimen from Tanzania and found that jaws were indeed present. He noted that he re-examined Alder and Hancock's specimen, but as the material was so poorly preserved, he could not determine whether jaws were present. In the same paper he indicated that jaws were absent in a specimen of *M. pilosa* he examined from Japan. Examination of material of all three species in the present study indicates that jaws were present in all specimens studied. In *M. pilosa* and *M. viridis*, the masticatory margin is smooth, while in *M. papillosa* it is denticulate. The specimens that Edmunds and Thompson identified as *M. pilosa* and Thompson and Crampton identified as *M. fimbriata* are clearly conspecific with *M. viridis* described here. The specimens described by Edmunds and Thompson and Thompson and Crampton clearly have multibranched papillae and dark rounded tubercles at the base of the cerata. These are characteristics found only in *M. viridis*. Their specimens have as many as 5 rows of papillae along the margin of the oral hood that is found only in *M. viridis* and *M. bucephala*. *Melibe pilosa* has a maximum of three rows of papillae while *M. papillosa* has only two rows.

Allan (1932) described *Propenelibe mirifica* as distinct species and genus. She stated that "[W]hile no anatomical studies have been undertaken from specimens collected in Australia...", published color photos from Queensland (Coleman 1989:61, middle photo) and Western Australia (Wells and Bryce 1993:175, lower photo) show large animals with distinct dark rounded tubercles and branched papillae that are diagnostic features of *M. viridis*. We therefore consider *P. mirifica* to be a junior synonym of *M. viridis*.

Kelaart's name, *Meliboea viridis,* has been largely ignored by subsequent authors. Rudman (1999) noted that Alder and Hancock stated that *M. viridis* was probably a juvenile of the animal that they named *M. fimbriata*, but objected to the name *viridis*, since their specimen was not greenish in color. Rudman stated that he could find no consitent basis for separating the two species. We

agree with Rudman and consider *M. fimbriata*, *M. vexillifera* and *M. mirifica* all to represent junior synonyms of *M. viridis*.

Species Taxonomy and Nomenclature

In the last review of the genus (Gosliner 1987) fifteen valid species were recognized. In the present study, three new species are described and *M. papillosa*, *M. pilosa* and *M. viridis* are recognized as distinct species. Several species have been incompletely described and have not been subsequently studied. *Melibe capucina* described from the Philippines (Bergh 1875) is not identifiable with any of the four species subsequently collected from the Philippines. Its taxonomic status remains uncertain. *Melibe japonica* Eliot, 1913 was not fully described and none of the anatomical features were illustrated. From the external description, it appears that this species may be synonymous with *M. viridis*. In the same paper, Eliot (1913) appears to have confused *M. vexillifera* (=*M. viridis*) with *M. papillosa*. *Melibe maugeana* Burn, 1960, on the basis of the illustrations of the rhinophores and cerata, appears to differ from the other temperate Australian species, *M. australis* (Angas, 1864). Details of its anatomy have not been described, nor has it been documented in collections since the original description. *Melibe mirifica* (Allan, 1932), considered as a valid species by Gosliner (1987), is here regarded as a junior synonym of *M. viridis*. *Melibe ocellata* Bergh, 1888 and *M. rangi* Bergh, 1875 were not completely described and have not been observed since their original descriptiona. Their taxonomic status remains uncertain.

On the basis of the present study, the following species appear to be distinct and recognizable:

Melibe australis (Angas, 1864)
Melibe bucephala Bergh, 1902
Melibe digitata Gosliner and Smith, n. sp.
Melibe engeli Risbec, 1937
Melibe leonina (Gould, 1852)
Melibe liltvedi Gosliner, 1987
Melibe maugeana Burn, 1960
Melibe megaceras Gosliner, 1987
Melibe minuta Gosliner and Smith, n. sp.
Melibe papillosa (de Filippi, 1867)
Melibe pilosa Pease, 1860
Melibe rosea Rang, 1829
Melibe tuberculata Gosliner and Smith, n. sp.
Melibe viridis (Kelaart, 1858) = *Melibe fimbriata* Alder and Hancock, 1864 = *Melibe vexillifera* Bergh, 1880 = *Proponelibe mirifica* Allan, 1932
= ? *Melibe japonica* Eliot, 1913

Doubtful species include the following:

Melibe capucina Bergh, 1875
Melibe ocellata Bergh, 1888
Melibe rangi Bergh, 1875

Phylogenetics

Character Analysis

In order to study the phylogenetic relationships of members of the Tethydidae and to test the monophyly of *Melibe*, a phylogenetic analysis has been undertaken. To examine these relationships

of these taxa, 47 anatomical characters were surveyed in 15 taxa. In addition to the thirteen taxa of *Melibe* included in this study, data for the other member of the Tethydidae, *Tethys fimbria* (Linnaeus, 1767) was examined. *Marionia* was used as the outgroup of the Tethydidae, since it represents one of the most basal members of the Dendronotacea (Odhner 1936).

The following characters were examined and coded (see also table [Fig. 24]):

1. *Body surface*: The body surface of the outgroup *Marionia* is ornamented with rounded tubercles. Members of the ingroup may have a smooth body surface (0), a surface with tubercles (1) or one with papillae (2).

2. *Foot width*: In the outgroup and some members of the ingroup the foot is moderately wide (1), while in some ingroup taxa the foot is narrow (0).

3. *Foot papillae*: In some species of *Melibe* a series of elongate papillae are present (1) on the anterodorsal surface of the foot. These structures are absent (0) in the outgroup, *Tethys* and several members of *Melibe*.

4. *Oral hood*: An oral hood is a distinctly expanded portion of the head that is used by members of the Tethydidae to capture crustacean prey. It absent (0) in the outgroup and present (1) in all members of the ingroup.

5. *Oral hood size*: This character is absent (2) within the outgroup and may be either a large (0) or small (1) structure within the Tethydidae.

6. *Oral hood margin*: This character is not applicable (?) to the outgroup. The oral hood margin within the ingroup may contain one row of papillae (0), two rows of papillae (1) or more than two rows of papillae (2).

7. *Oral hood papillae*: This character is not applicable (?) to the outgroup. In the ingroup the papillae on the oral hood are equal in length (0), the inner row is longest or the outer row is longest.

8. *Papillae on oral hood*: This character is not applicable (?) within the outgroup. Papillae may be either absent (0) or present (1) on the surface of the hood in members of the ingroup.

9. *Rhinophores*: The rhinophores are chemosensory organs situated on either side of the dorsal surface of the head. They are present in all taxa studied here. In the outgroup and most members of the ingroup the bases of the rhinophores are well-separated from each other (0). In *M. digitata* and *M. tuberculata* they are adjacent (1) to each other.

10. *Rhinophore sheath sail*: In the outgroup and most members of the ingroup the posterior end of the rhinophore sheath lacks any posterior extension (0). In some members of the ingroup the posterior end of the sheath has a membranous, sail-like extension (1).

11. *Rhinophore sheath papilla*: In some members of the ingroup a distinct papilla is present at the apex of the posterior end of the rhinophore sheath (1). It is absent in *Marionia* and many members of the ingroup (0).

12. *Gills*: A series of dendritic respiratory structures are found on the lateral margins of the notum in the outgroup and in *Tethys* (0), but are absent (1) in species of *Melibe*. These structures have often been called gills, but are not homologous to the ctenidium of other mollusks.

13. *Cerata*: Elongate appendages are found on the lateral margins of the members of the ingroup (1). These structures, generally called cerata, often contain branches of the digestive gland. They are absent (0) from members of the outgroup.

14. *Ceratal shape*: Ceratal shape is not applicable (?) to the outgroup. Within the ingroup, the cerata may be either inflated (0) or laterally flattened (1).

15. *Ceratal tubercles*: In many ingroup taxa the surface of the cerata bears rounded tubercles (1). Other members of the ingroup lack tubercles on the cerata (0). This character is not applicable to the outgroup (?).

16. *Cerata1 papillae*: This character is not applicable (?) to the outgroup, since species of *Marionia* lack cerata. Some ingroup members lack elongate papillae on the surface of the cerata (0), while they are present in others (1). This character is independent of the previous one, since some taxa may have both tubercles and papillae.

17. *Genital opening*: In the outgroup the genital aperture has no distinct papillae with which they are associated (0). In some members of the ingroup, there are no distinct papillae, or 3 or less papillae, which is also coded as absent (0). In other ingroup taxa there are distinct papillae around the margin of the genital atrium, arranged in a circular manner (1).

18. *Inner oral hood surface*: In *Marionia*, this character is not applicable since and oral hood is not present (?). In members of the ingroup an oral hood is present and its inner surface is either smooth (0), finely papillate (1), or coarsely papillate (2).

19. *Mouth surface*: In the outgroup and some members of the ingroup the surface of the tissue surrounding the oral opening is smooth (0). In some ingroup taxa it bears a series of papillae around the opening (1). Presumably, these papillae serve a sensory function.

20. *Buccal mass*: In the outgroup and most members of the ingroup, the buccal mass is wide (0). In *M. digitata* it is of intermediate width (2), while in *M. minuta* it is narrow (1). This multistate character is treated as unordered.

21. *Jaws*: In the outgroup a pair of jaws with a denticulate masticatory margin is present (0). In members of the ingroup, the jaws may be denticulate, have a smooth masticatory margin (1), or be entirely absent (2).

22. *Salivary glands*: In the outgroup and several members of the ingroup a pair of elongate salivary glands is present on either side of the junction of the esophagus with posterior end of the buccal mass (1). In several ingroup taxa, the salivary glands are compact (0). In *M. australis* salivary glands appear to be entirely absent (2).

23. *Esophagus*: In the outgroup and some members of the ingroup the esophagus, between the posterior end of the buccal mass and the stomach, is a relatively short duct (0). In a few ingroup taxa the esophagus is more elongate (1).

24. *Stomach plates*: In the outgroup taxon the stomach contains more than 20 chitinous plates that are presumably used to crush the calcareous sclerites of cnidarian prey (2). The ingroup taxa feed on crustaceans. Many of them have 20 or more stomach plates, some have 10–19 plates (1), some have fewer than 10 plates (0) and in others plates are entirely absent (3).

25. *Stomach plate alignment*: In the outgroup and several members of the ingroup the apices of the chitinous plates that line the stomach are all aligned with the highest point near the middle (0). In some members of the ingroup the apices of the plates alternate in position from the right and left side of the median line (1).

26. *Stomach plate size*: In the outgroup and in some members of the ingroup, the stomach plates are more or less uniform in size (0). In other ingroup taxa the plates alternate between large and small plates (1).

27. *Stomach plate shape*: In the outgroup and some members of the ingroup, the stomach plates are bilaterally symmetrical with a apex in the middle of the plate (0). Other members of the ingroup have plates with an eccentric apex (1).

28. *Digestive gland:* In the outgroup and several members of the ingroup, the digestive gland forms a compact mass (0) while in other ingroup members it is more diffuse (1).

29. *Digestive gland enters first cerata*: In the outgroup the digestive gland does not extend to the dorsal surface (2). In some of the ingroup taxa the digestive gland penetrates less than the basal half of the cerata (1), while in others it penetrates well beyond the middle of each ceras (0).

30. *Digestive gland branches*: In the outgroup the digestive gland forms a solid mass that is

not ramified (2). In the ingroup taxa the digestive gland is always ramified. In some cases it is ramified only within the cerata (1), in others it is ramified around the stomach and in the cerata (0).

31. *Posterior digestive gland branch*: In *Marionia* and most ingroup taxa the posterior branch of the digestive gland is well developed (0). In a few members of the ingroup this posterior branch is poorly developed (1).

32. *Posterior digestive gland entry*: In the outgroup, the posterior digestive gland does not extend dorsally towards the notal surface (2). In the ingroup, the posterior branch of the digestive gland extends dorsally and enters some of the posterior cerata. In some cases it enters all of the cerata (3), in others only the anteriormost pair of post-cardiac cerata (0) and in other cases only the anterior 2 post-ceratal pairs (3).

33. *Ganglia*: *Marionia*, the outgroup taxon, has ganglia with a smooth external margin (0). In members of the ingroup the ganglia may be smooth or have an irregular outline due to presence of large peripheral nerve cells (1).

34. *Pleural ganglia*: In the outgroup and most members of the ingroup the pleural ganglia are well-separated from the cerebral ganglia (0), while in some members of the ingroup these ganglia are largely fused (1).

35. *Pedal commissure*: In the outgroup and the majority of members of the ingroup, the commissure joining the pedal ganglia is elongate (1). In a few taxa this commissure is short (0).

36. *Buccal ganglia*: In the outgroup and many ingroup members, the buccal ganglia are well-separated from each other (1). In some ingroup members the ganglia are adjacent to each other (2) or, in other cases, they actually touch each other (0).

37. *Buccal ganglia texture*: In the outgroup and virtually all members of the ingroup the buccal ganglia have a smooth texture (0), while in *M. viridis*, the ganglia appear tuberculate (1) owing to the presence of large peripheral nerve cells.

38. *Ovotestis follicles:* In the outgroup and several ingroup taxa the ovotestis follicles are united in compound masses (2). In some ingroup taxa the follicles are only somewhat (two or three follicles together some or all of the time) compound (0) or form simple masses (1).

39. *Ovotestis development*: In the outgroup and several members of the ingroup, the follicles form a solid mass (2). In other ingroup members the follicles are either congested (0) or well separated (1).

40. *Receptaculum seminis*: In the outgroup and *Tethys*, a receptaculum seminis is indistinct (2). In members of the ingroup a distinct receptaculum seminis is present. It may be either serial (1), or enter via a distinct duct, where it is termed semi-serial (0).

41. *Serial receptaculum seminis*: In some ingroup taxa with a serial receptaculum seminis, the receptaculum may be either narrow (0) or expanded (1). This character is not applicable in the outgroup and in several of the ingroup taxa (?).

42. *Bursa copulatrix*: The bursa copulatrix of the outgroup and several members of the ingroup is pyriform (1). In a few ingroup taxa the bursa is spherical (0).

43. *Vaginal gland*: In the outgroup, a distinct vaginal gland is absent (0). In some members of the ingroup a gland is present. It may be either external and nodular (2) or internal and smooth (1). This multistate character is treated as unordered.

44. *Prostate gland*: In *Marionia* the vas deferens lacks a distinctly thickened prostate gland (0). In all of the ingroup members a distinct prostate is present (1).

45. *Penis*: In the outgroup and the vast majority of ingroup taxa, the penis is conical (0). In *Melibe leonina* the penis is elongate (1), while in *M. megaceras* the penis is flattened and paddle-shaped (2).

46. *Accessory penial sac*: In the outgroup and most members of the ingroup, the accessory

penial sac is absent (0). In *Tethys fimbria* an accessory sac is present (1).

47. *Zooxanthellae*: Members of the outgroup and some members of the ingroup lack brownish pigment and apparently lack zooxanthellae as symbionts (0). All of the tropical species of *Melibe* have brownish pigment and it has been demonstated that in the two species examined histologically (Kempf 1984) that this is due to the presence of zooxanthellae (1).

Phylogenetic Analysis

It was decided that species for which there was insufficient data would be excluded from the analysis. These were species for which no type material was available for comparison with the existing literature. This resulted in the exclusion of *M. capucina* Bergh, 1875; *M. ocellata* Bergh, 1888; *M. maugeana* Burn, 1957 and *M. rangi* Bergh, 1875. *Tethys fimbria* (Linnaeus, 1767) was included in the matrix, as it is the best described member of the second genus in the family Tethydidae. The genus *Marionia* was used as the outgroup. This analysis was performed using PAUP 3.1.1, with MacClade 3.01 for the data matrix. This resulted in an analysis of 15 taxa, using 47 characters. All characters were treated as un-ordered and unweighted. Heuristic search and branch and bound searches were undertaken using the DELTRAN option, resulting in a single tree with a length of 123 steps, a consistency index of 0.569 and retention index of 0.671 (Fig. 25).

Discussion

The resultant phylogeny supports the hypothesis that *Melibe* represents a monophyletic taxon. The four most basal species in the tree are all found in temperate regions, (California, South Africa and Australia, respectively) while the large more derived, monophyletic clade consists of all of the tropical Indo-Pacific species. This pattern of distribution, with basal temperate species and derived tropical ones, is consistent with what is seen with other groups of nudibranch molluscs, eg. *Flabellina* (Gosliner and Kuzirian 1990), *Hallaxa* (Gosliner and Johnson 1994) and *Platydoris* (Dorgan, Valdés, and Gosliner 2002). The most basal taxon within *Melibe* is *M. leonina*. This species retains more plesiomorphic attributes but has also several autapomorphies, related to most organ systems. *Melibe rosea* and *M.liltvedi*, both from South Africa, are sister taxa at the next highest node. They share apomorphies of their reproductive and nervous systems. The other temperate species, *M. australis* is the sister species to all of the Indo-Pacific taxa. This species has two autapomorphies, the absence of jaws and salivary glands. Kempf (1984) described the presence of zooxanthellae in some tropical species of *Melibe*. It appears that all members of the Indo-Pacific clade share the apomorphy of having zooxanthellae in their tissues. This may be an adaptation to living in less productive tropical waters. Within this clade there are certain morphological adaptations which may support the utilization of zooxanthelae. These include a transparent or highly translucent body allowing good light transmission to the symbionts, and cerata that are arranged in an alternating pattern that minimizes shading and optimizes control of light intensity. In addition, the members of this clade all have branches of the digestive gland within the cerata. While this relationship has not been studied, the digestive gland branches might aid in the transport of ingested symbionts to the ceratal tissues, and in the uptake of photosynthetic products by the host. The transparency of these animals, along with the color imparted by the symbiont may also provide many of these species with a high degree of crypsis, allowing them to almost disappear against their normal background. The Indo-Pacific clade has undergone considerable speciation, with nine recognized nominal species.

The biogeographical relationships of the Indo-Pacific taxa are complex and sister taxa do not

exhibit markedly vicariant distributions. In both cases where sister taxa are well defined, the sister species are sympatric, for at least a portion of their ranges. *Melibe viridis* is one of the most widespread species, known from the western Indian Ocean to the western Pacific. In the Red Sea and the Gulf of Thailand it is found sympatrically with its sister species, *M. bucephala*. The other pair of sister species, *M. digitata* and *M. tuberculosa*, is sympatric in the Philippines. Knowledge of distributional ranges of many species is likely incomplete. Since *M. megaceras* was first described from the Hawaiian Islands (Gosliner 1987), two additional specimens have been recorded here from Dubai and Indonesia, greatly extending the known distribution of this species. *Melibe engeli* has only been observed a few times since its original description, although it can be sporadically abundant in some habitats (present study). Several species have never been recorded since their original descriptions and their systematic and biogeographical status remain in doubt. Incomplete records of other species may greatly impact our understanding of natural ranges for species of *Melibe*. The cryptic color patterns and small body size of many species likely compound our poor knowledge of these distributional patterns.

The Tethydididae are highly modified dendronotoideans. All species of both *Tethys* and *Melibe* have lost the radula and in many taxa the jaws are also reduced or entirely lost. Most dendronotoideans are specialized predators upon coelenterates (McDonald and Nybakken 1999). In contrast, species of *Melibe* and *Tethys* are predators upon crustanceans and have altered their external body form and digestive system to accommodate this dietary modification.

Acknowledgments

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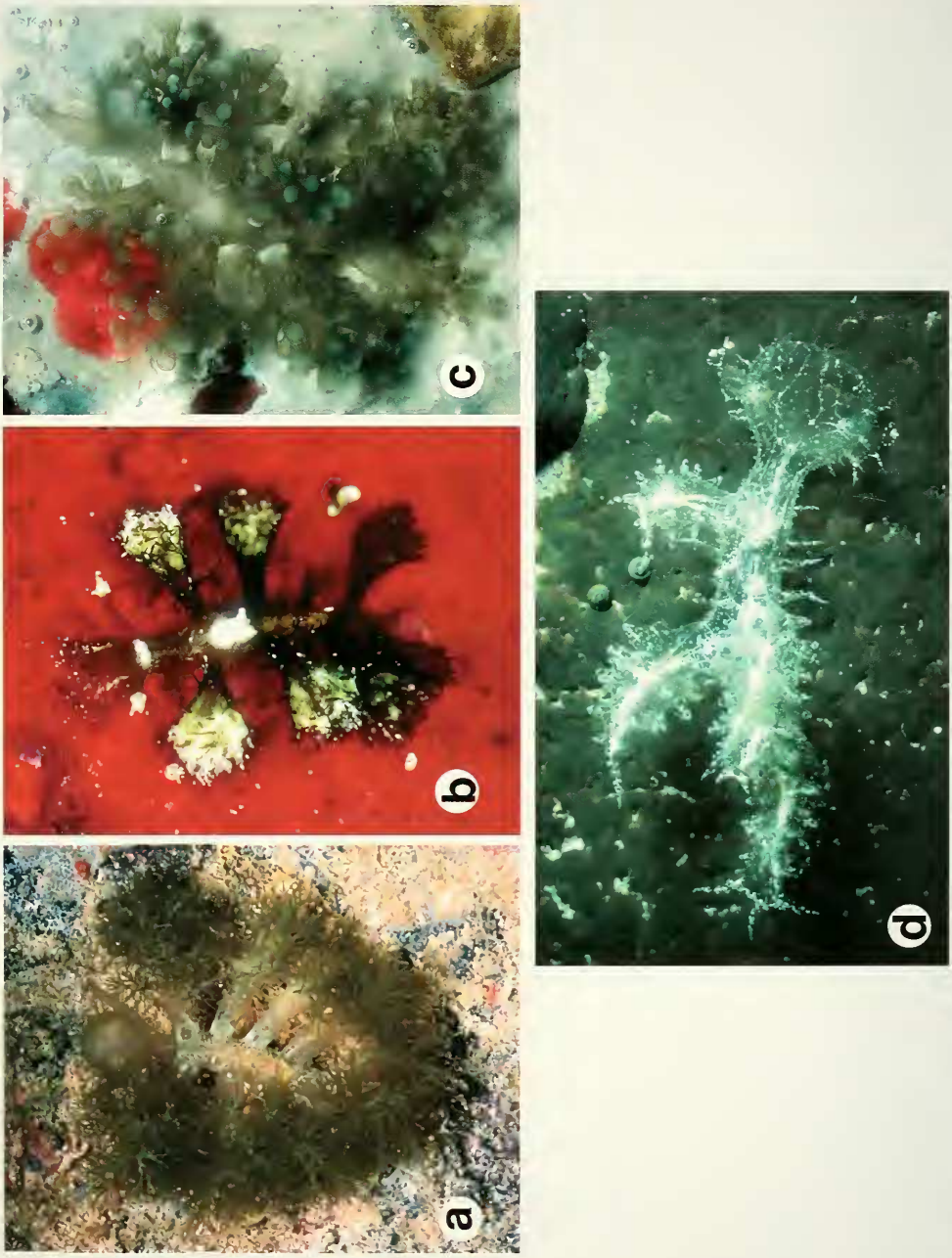

Figure 1. Photographs of living animals. A: *Melibe digitata* sp. nov. B: *Melibe minuta* sp. nov. C: *Melibe tuberculata* n. sp.. D: *Melibe engeli* Risbec, 1951.

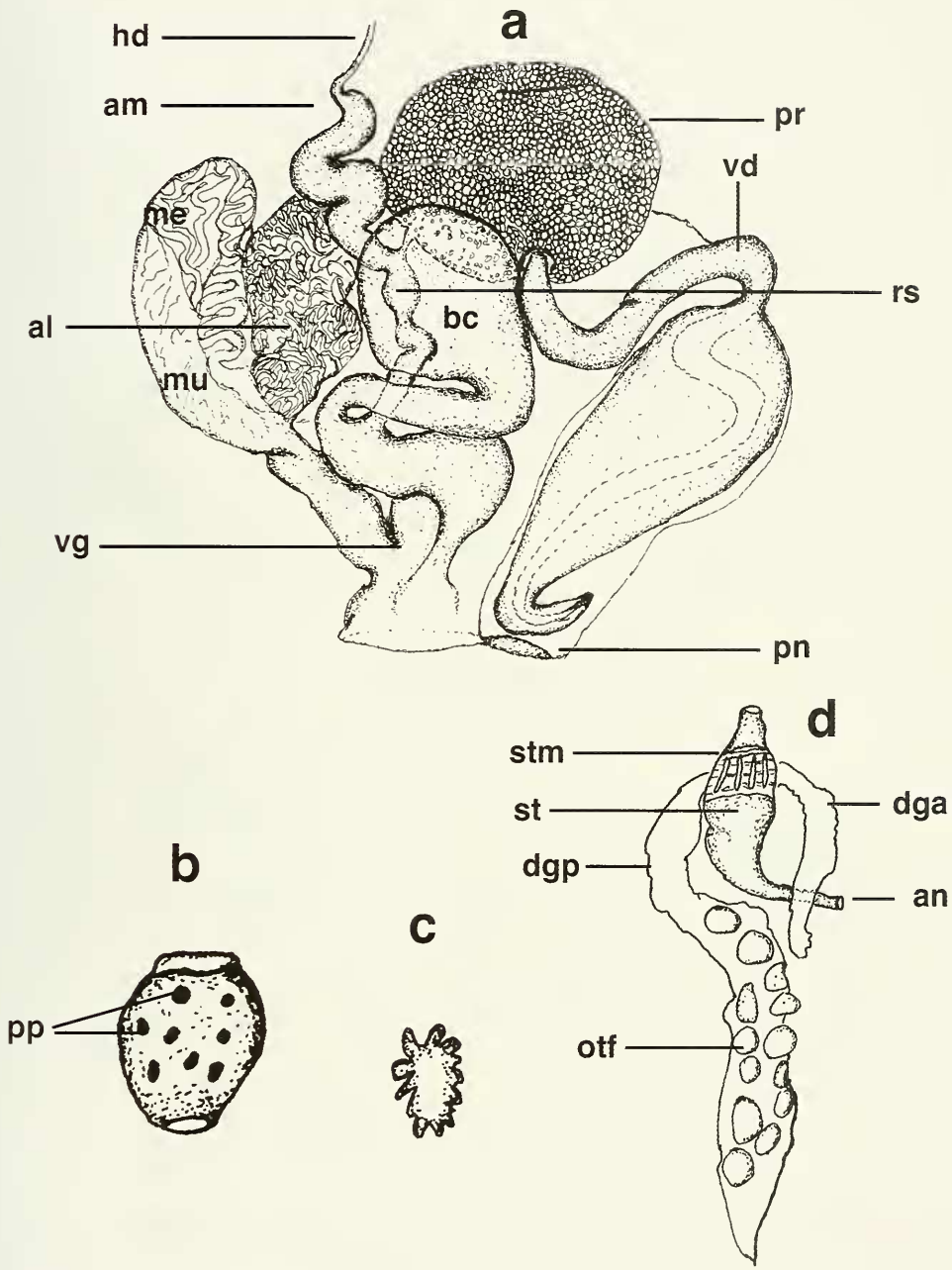

FIGURE 2. *Melibe bucephala* Bergh, 1902, anatomy (BMNH1933.6.30.35). A: Reproductive system. al = albumen gland; am = ampulla; bc = bursa copulatrix; hd = hermaphroditic duct; me = membrane gland; mu = mucous gland; pn = penis; pr = prostate gland; rs = receptaculum semenis; vd = vas deferens; vg = vaginal gland. B: Buccal mass. pp = papillae. C: Portion of viscera. An = anus; dga = anterior digestive gland; dgp = posterior digestive gland; otf = ovotestis follicles; st = posterior portion of stomach; stm = muscular portion of stomach. D: portion of central nervous system.

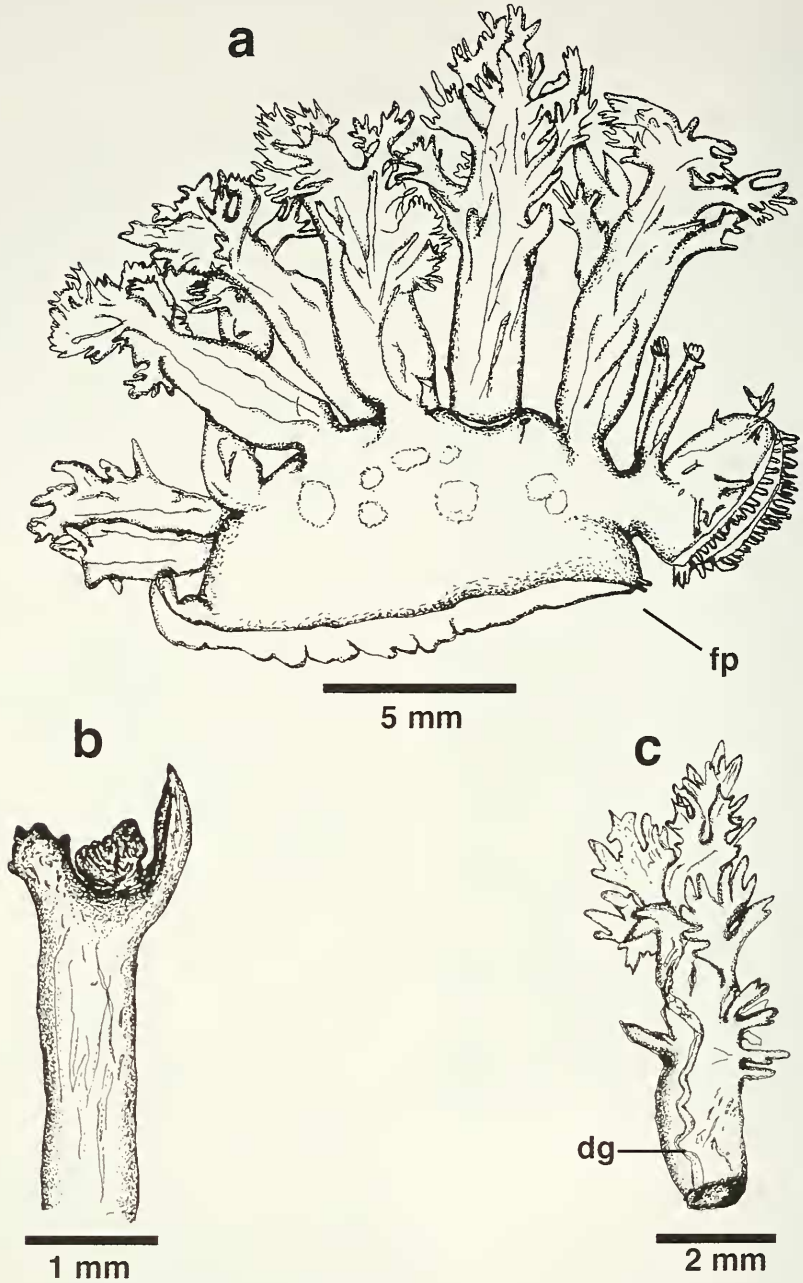

FIGURE 3. *Melibe digitata* sp. nov., morphology. A: Body of preserved specimen (CASIZ 110425). fp = foot papillae. B: Rhinophore (CASIZ 103754). C: Detached ceras (CASIZ 103754).

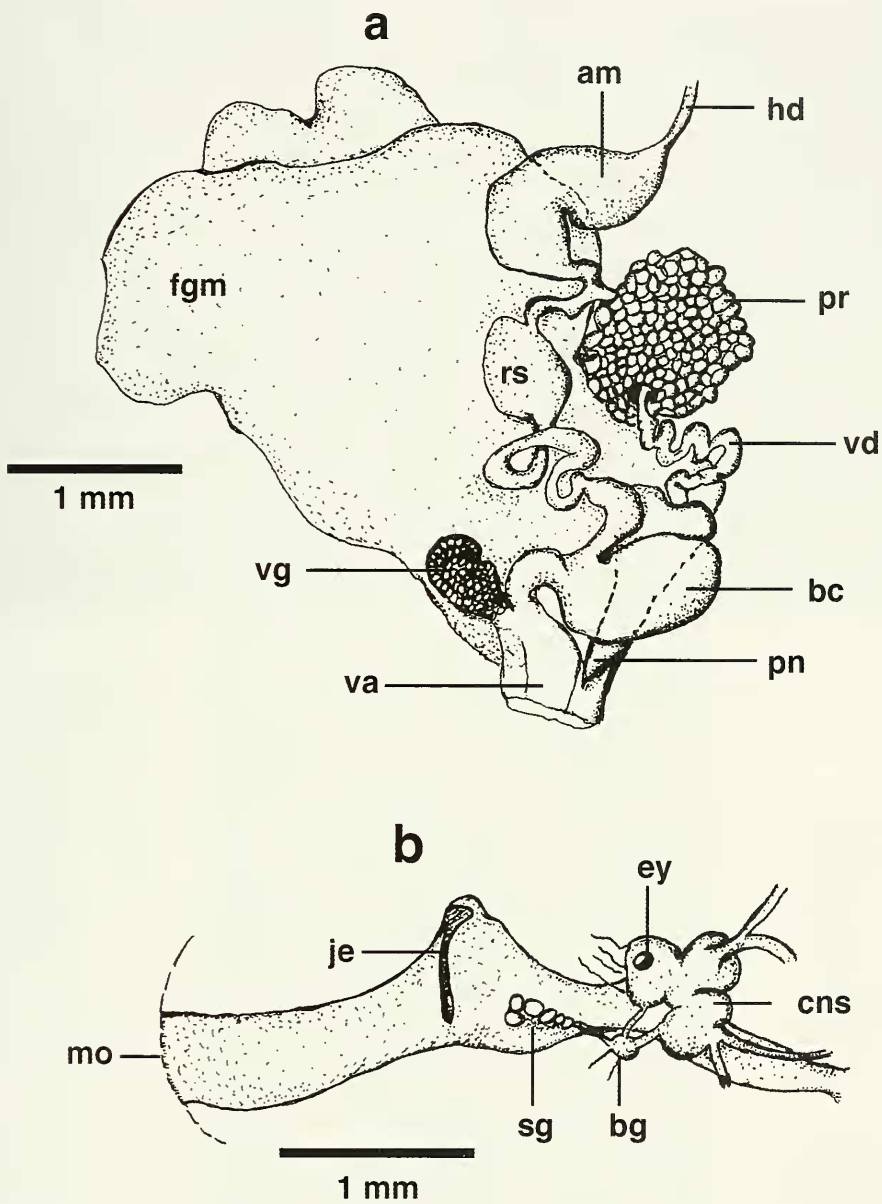

FIGURE 4. *Melibe digitata* sp. nov., anatomy (CASIZ 110425). A: Reproductive system. am = ampulla; bc = bursa copulatrix; fgm = female gland mass; hd = hermaphroditic duct; pn = penis; pr = prostate; rs = receptaculum semenis; va = vaginal atrium; vd = vas deferens; vg = vaginal gland. B: Buccal mass. bg = buccal ganglia; cns = central nervous system; ey = eye; je = jaw edge; mo = mouth; sg = salivary glands

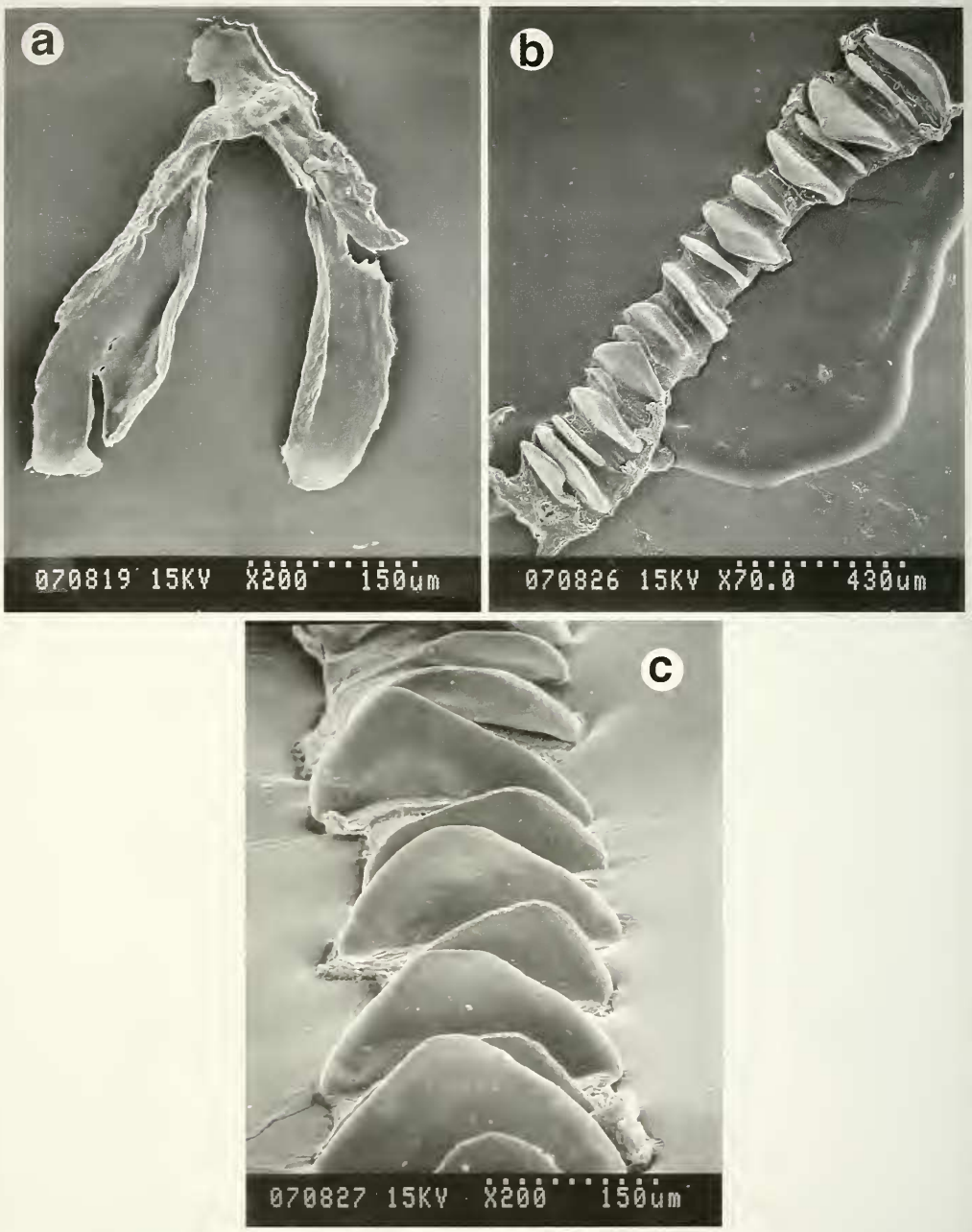

FIGURE 5. *Melibe digitata* sp. nov. (CASIZ 110425). A: Jaws. B-C: Stomach plates.

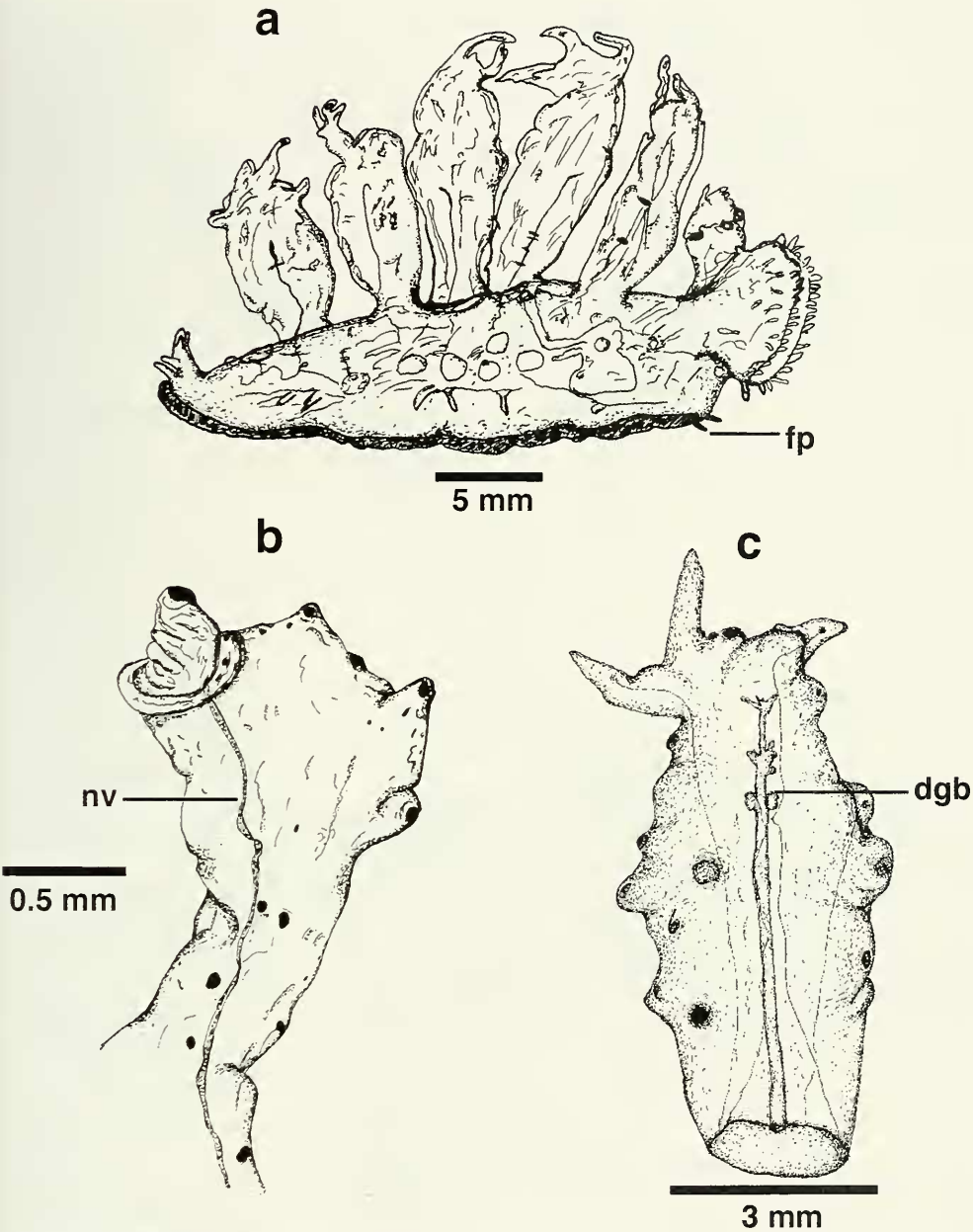

FIGURE 6. *Melibe engeli* Risbec, 1937, morphology. A: Body of preserved specimen (CASIZ 110389). fp = foot papillae. B: Rhinophore CASIZ 106396). nv = nerve. C: Detached ceras (CASIZ 93676). dgb = branch of digestive gland.

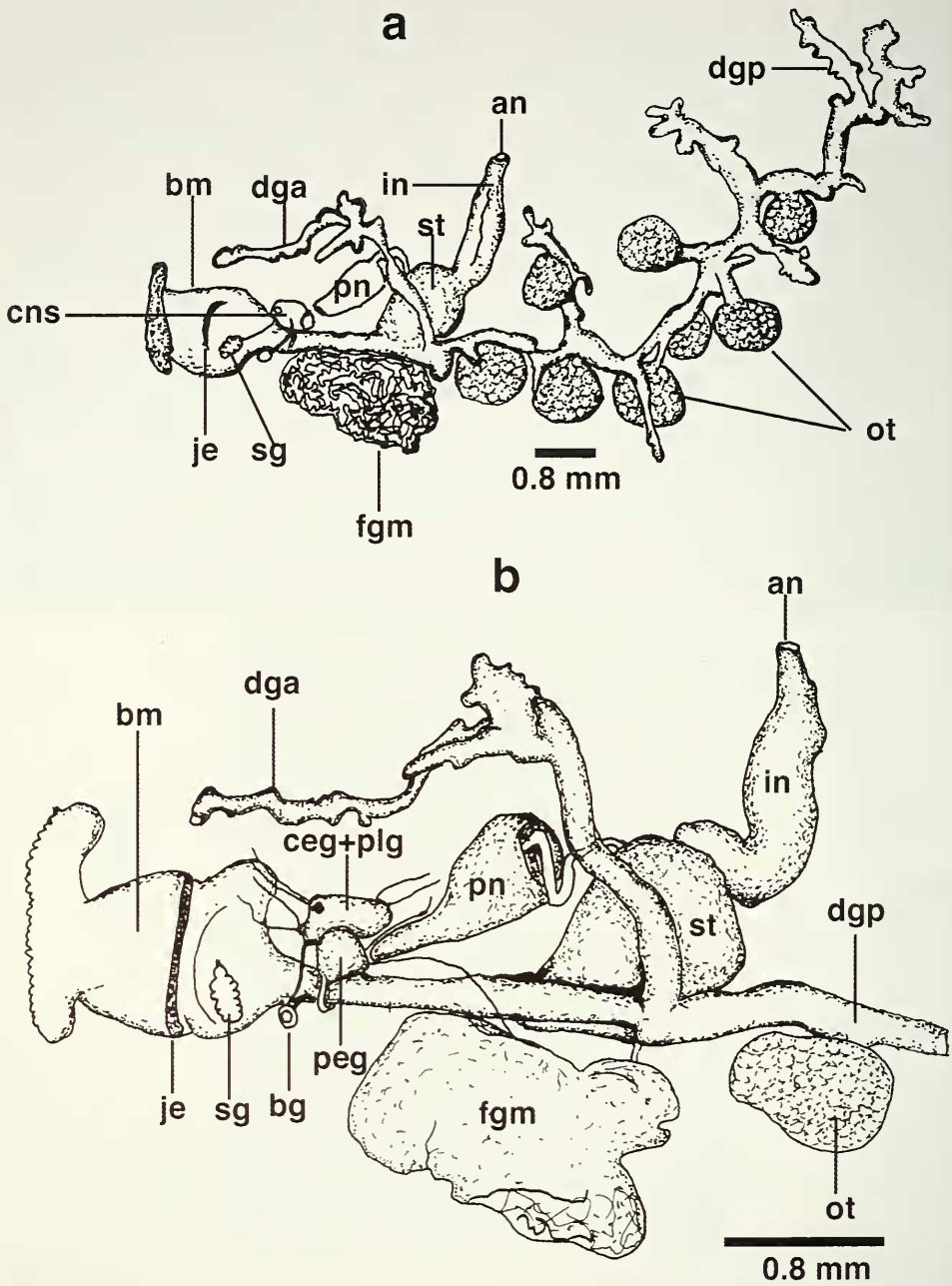

FIGURE 7. *Melibe engeli*, two views of visceral mass (CASIZ 105680). A: Visceral mass removed nearly intact. B: Close up view of anterior portion. an = anus; bg = buccal ganglia; bm = buccal mass; ceg = cerebral ganglia; cns = central nervous system; dga = anterior digestive gland; dgp = posterior digestive gland; fgm = female gland mass; in = intestine; je = jaw edge; ot = ovotestis; peg = pedal ganglia; plg = pleural ganglia; pn = penis; sg = salivary gland, st = stomach.

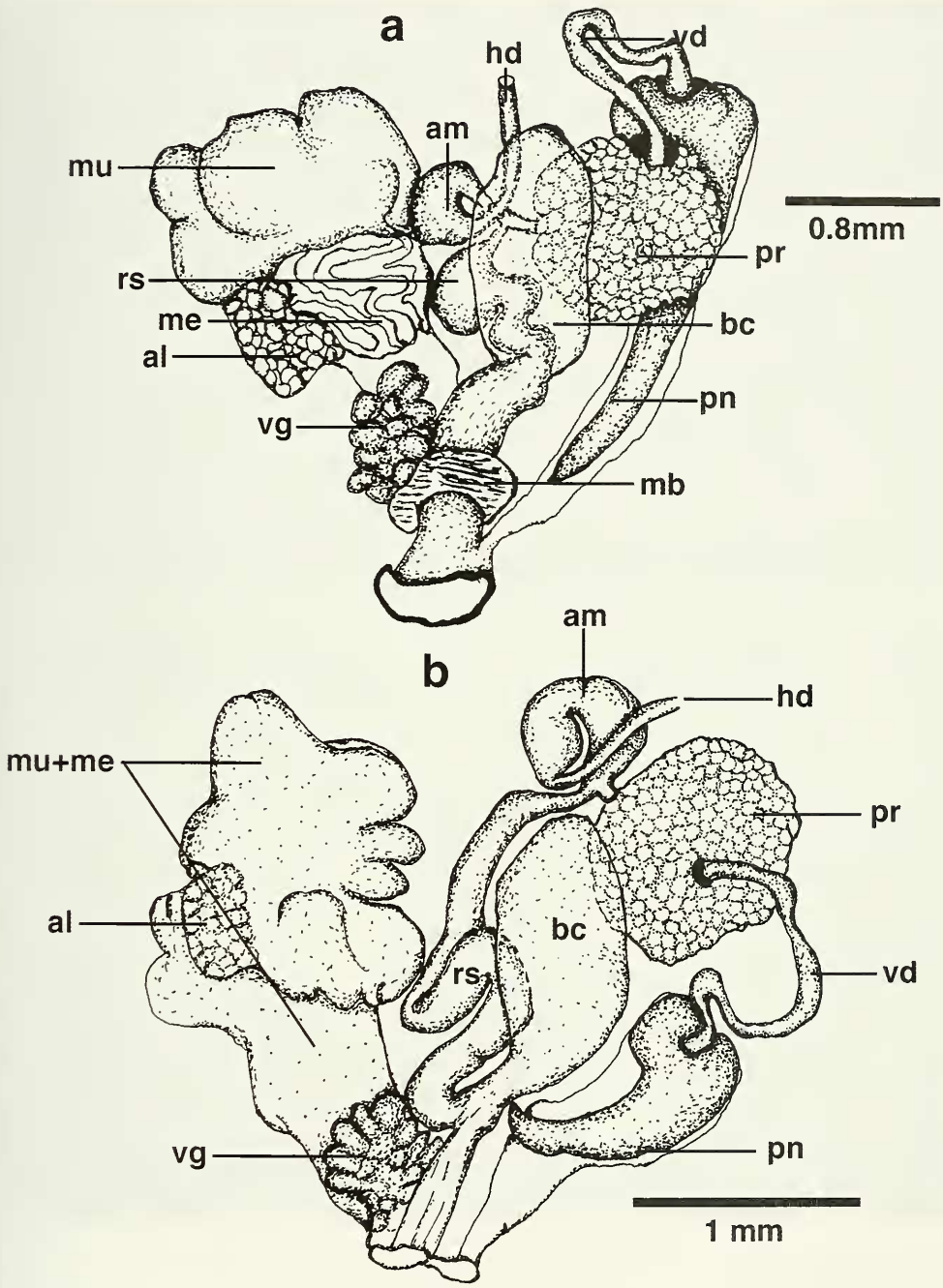

FIGURE 8. *Melibe engeli*, comparison of reproductive systems. A: Philippine specimen (CASIZ 105680). B: Hawai'ian specimen (CASIZ 89652). al= albumen gland; am = ampulla; bc = bursa copulatrix; mb = muscular band; me = membrane gland; mu = mucous gland; pn = penis; pr = prostate; rs = receptaculum semenis; vd = vas deferens; vg = vaginal gland.

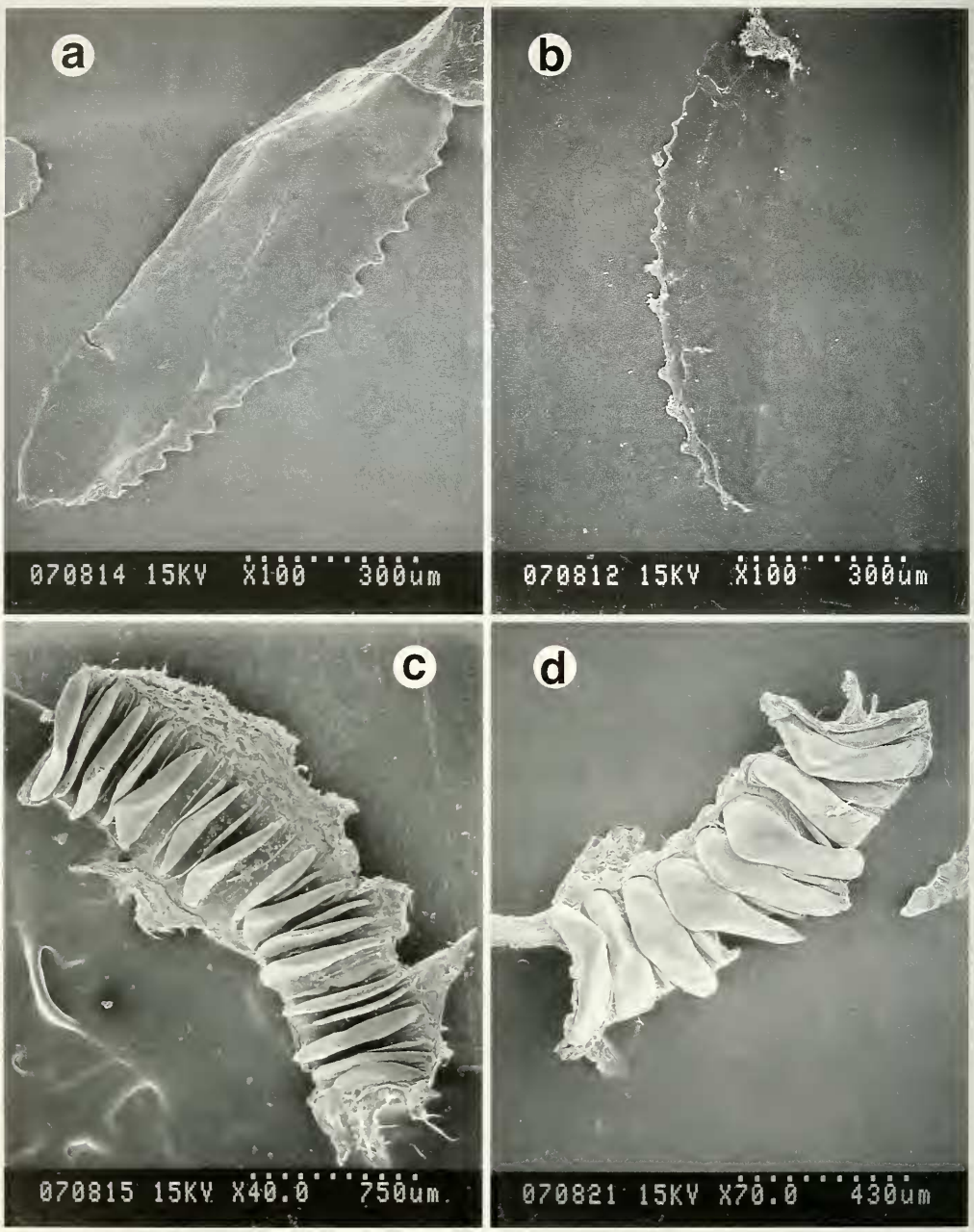

FIGURE 9. *Melibe engeli*, comparison of digestive armature. A: Jaw of CASIZ 89652 (Hawai'i). B: Jaw of CASIZ 105680 (Philippines). C: Stomach plates of CASIZ 89652. D:Stomach plates of CASIZ 105680.

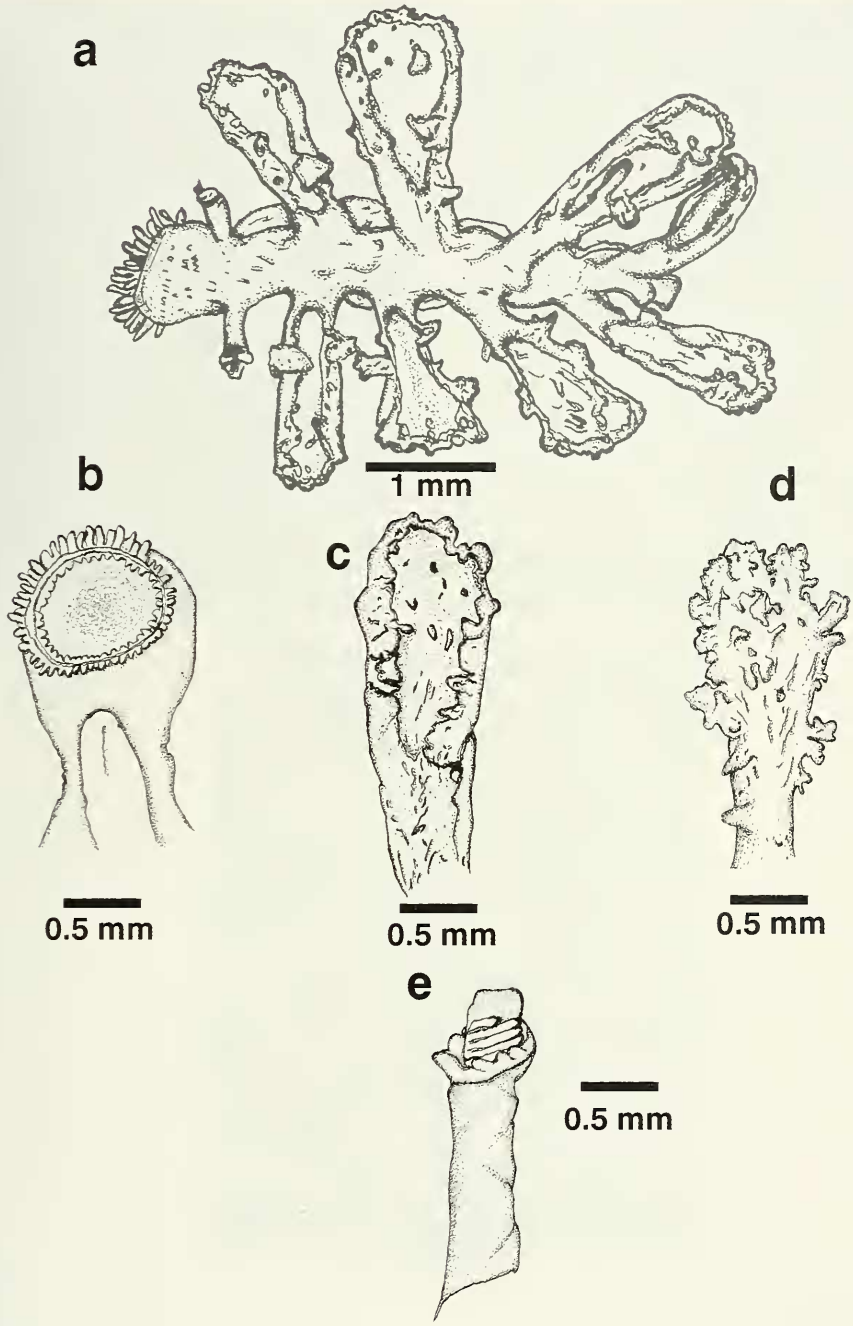

FIGURE 10. *Melibe minuta* sp. nov., External morphology. A: Dorsal view of animal (CASIZ 78517). B: Ventral view of oral hood, mouth, and anterior foot (CASIZ 78533). C: Detail of inward facing surface of ceras CASIZ 78529). D: Detail of outward facing side of ceras (CASIZ 78529). E: Detail of rhinophore (CASIZ 78517).

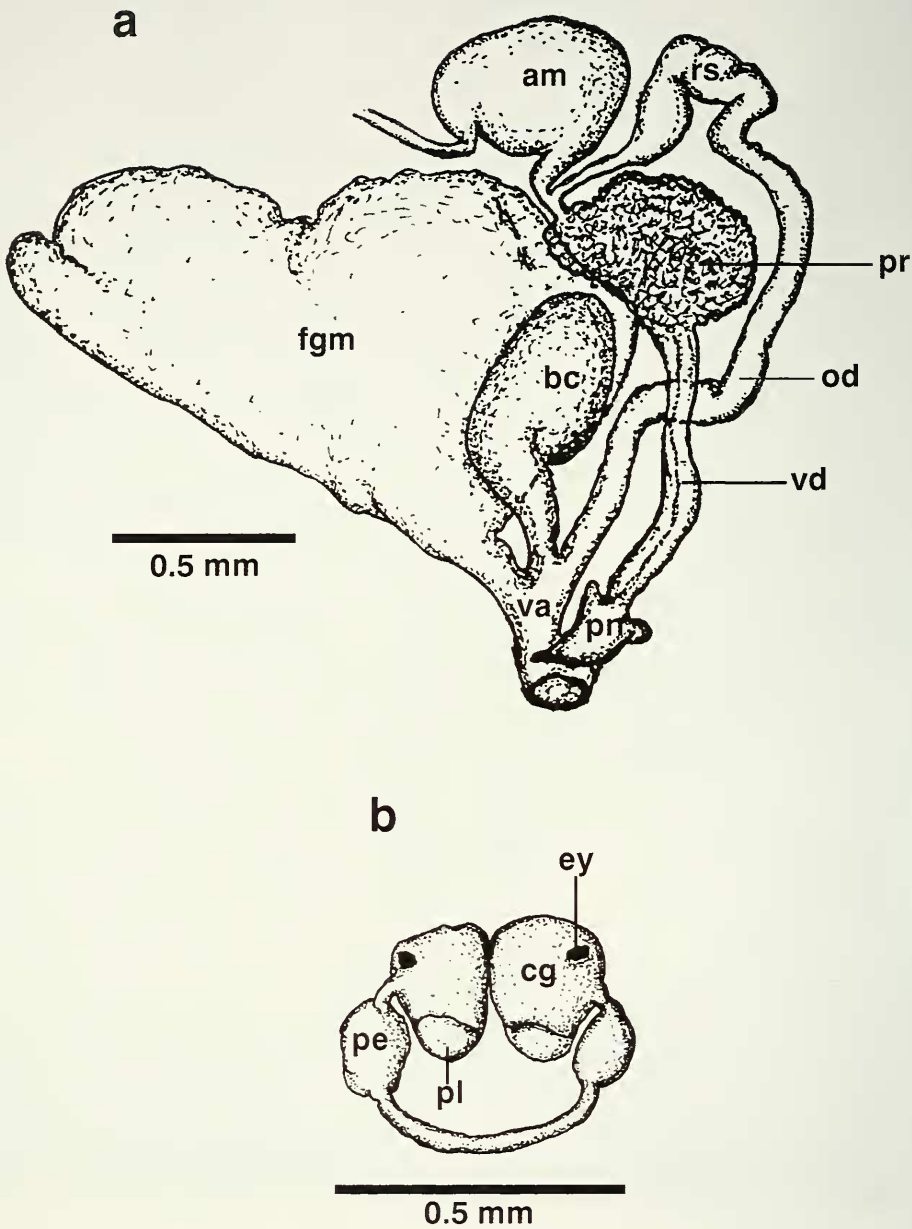

FIGURE 11. *Melibe minuta* sp. nov., anatomical details. A: Reproductive system (CASIZ 78533). B: Central nervous system. am = ampulla; bc = bursa copulatrix; cg = cerebral ganglion; ey = eye; fgm = female gland mass; od = oviduct; pe = pedal ganglion; pl = pleural ganglion; pn = penis; pr = prostate; rs = receptaculum semenis; va = vagina; vd= vas deferens.

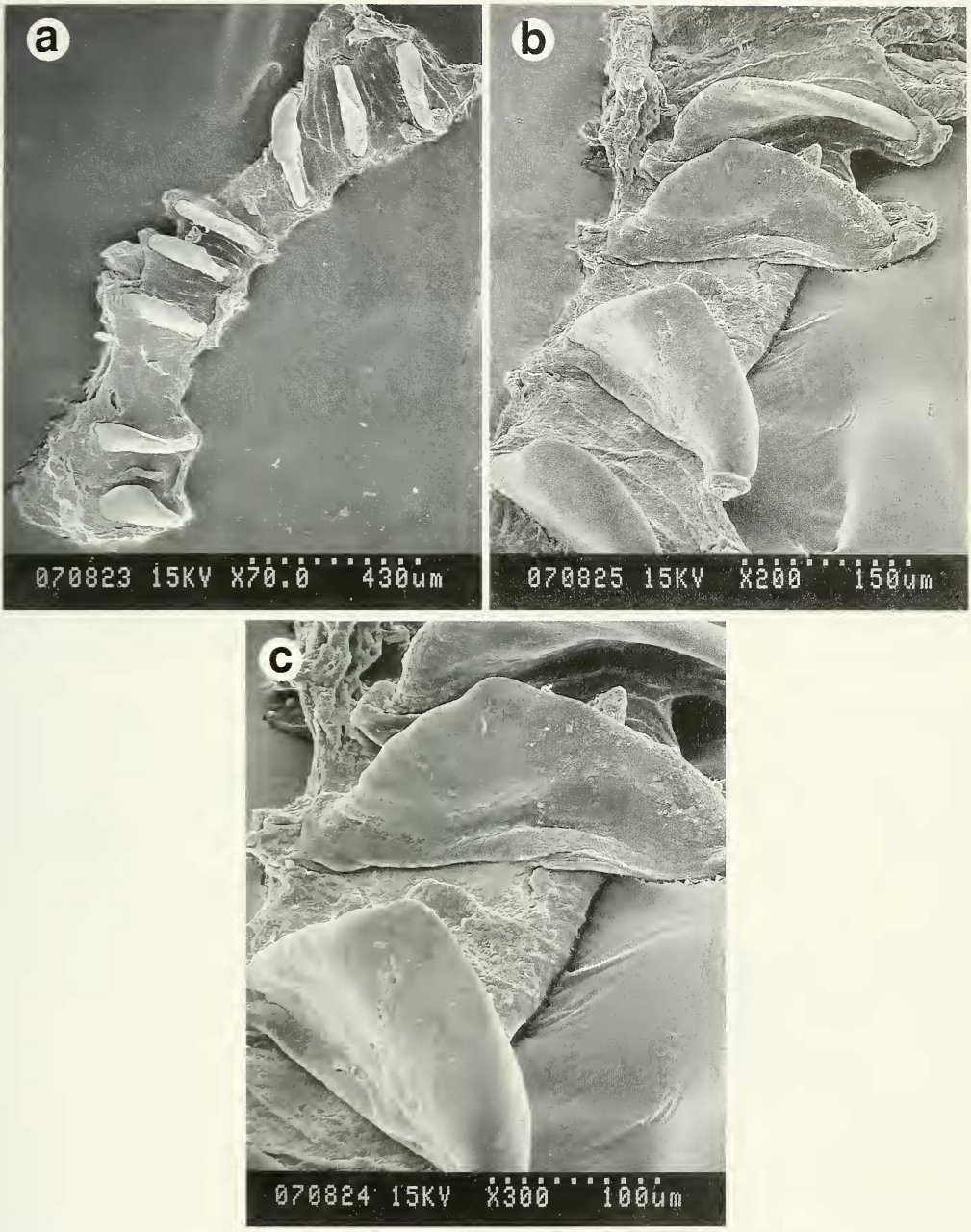

FIGURE 12. *Melibe minuta* sp. nov., SEM's of stomach plates (CASIZ 87918). A: Entire band of stomach plates. B-C: Details of stomach plates.

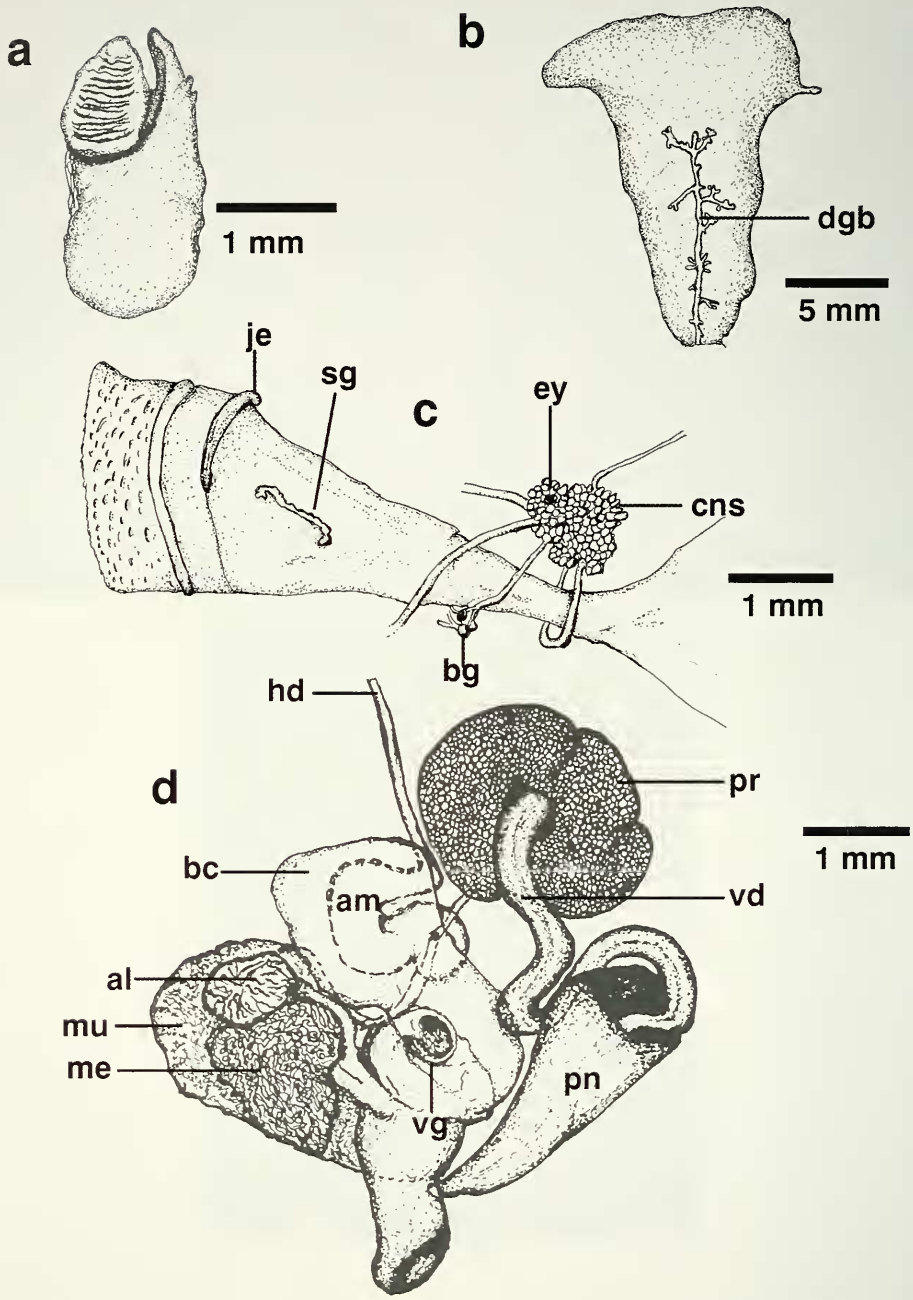

FIGURE 13. *Melibe papillosa* (de Filippi, 1867), morphology and anatomy (CASIZ 89005). A: Rhinophore. B: Ceras. C: Buccal mass and central nervous system. D: Reproductive organs. am = ampulla; al = albumen gland; bc = bursa copulatrix; bg = buccal ganglia; cns = central nervous system; dgb = digestive gland branch; ey = eye; je = jaw edge; me = membrane gland; mu = mucous gland; pn = penis; pr = prostate; sg = salivary gland; vd = vas deferens; vg = vaginal gland.

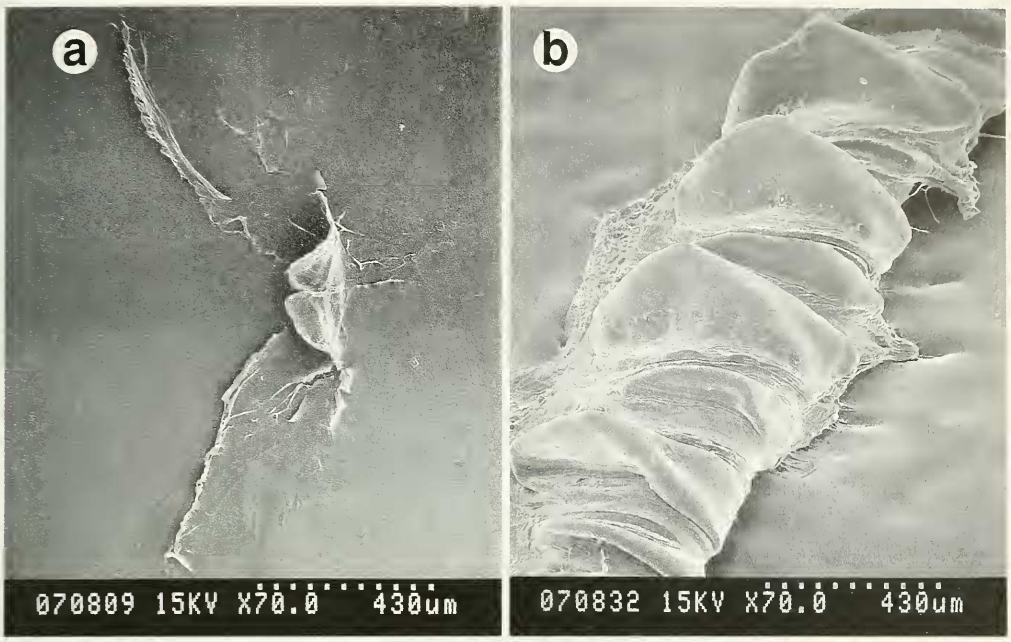

FIGURE 14. *Melibe papillosa*, digestive armature (CASIZ 89005). A: Jaws. B: Stomach plates.

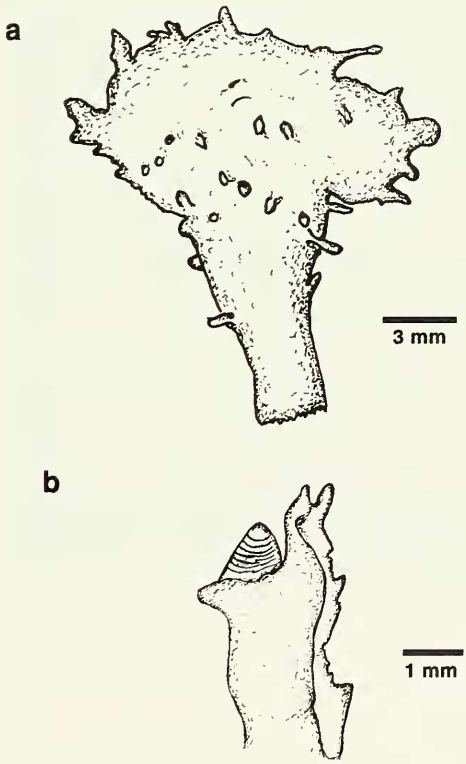

FIGURE 15. *Melibe pilosa* Pease, 1860, external morphology. A: Detail of ceras (CASIZ 61501). B: Detail of rhinophore (CASIZ 16677).

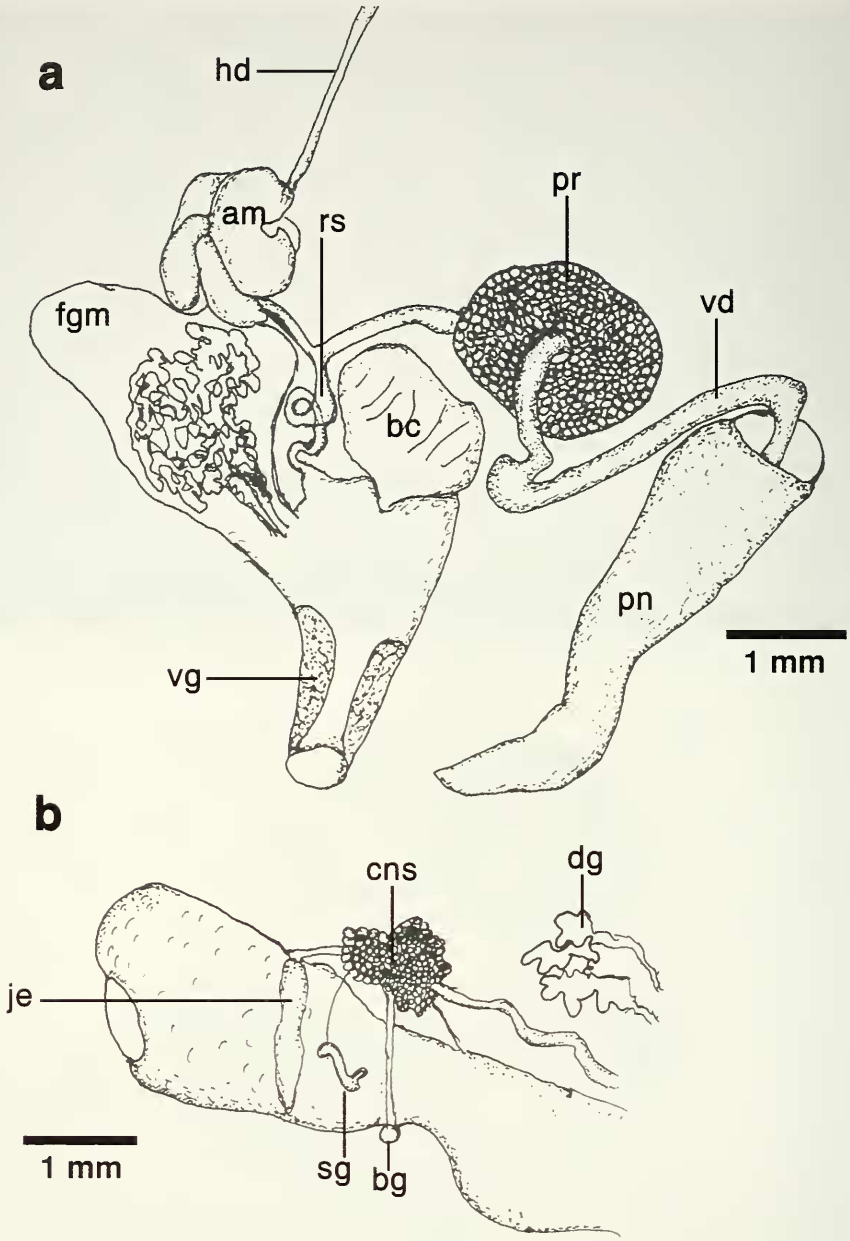

FIGURE 16. *Melibe pilosa*, anatomy. A: Reproductive organs (CASIZ 61516). B: Buccal mass and anterior visceral organs CASIZ 16677). am = ampulla; bc = bursa copulatrix,; bg = buccal ganglia; cns = central nervous system; dg = digestive gland; fgm = female gland mass; hd = hermaphroditic duct; je = jaw edge; pn = penis; pr = prostate; rs = receptaculum semenis; sg = salivary gland; vd = vas deferens; vg = vaginal gland.

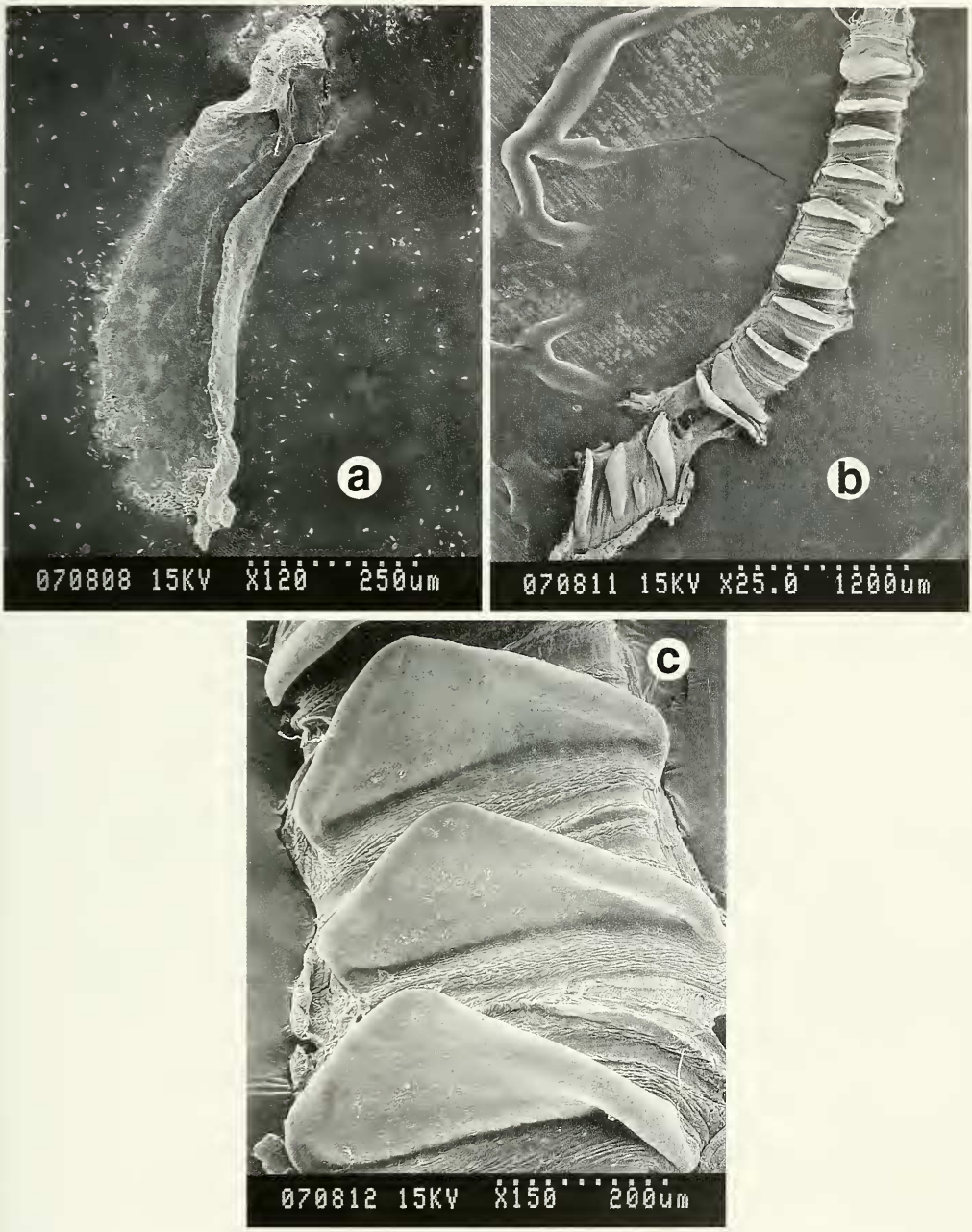

FIGURE 17. *Melibe pilosa*, digestive armature (CASIZ 61506). A: Jaws. B: Girdle of stomach plates. C: Detail of stomach plates.

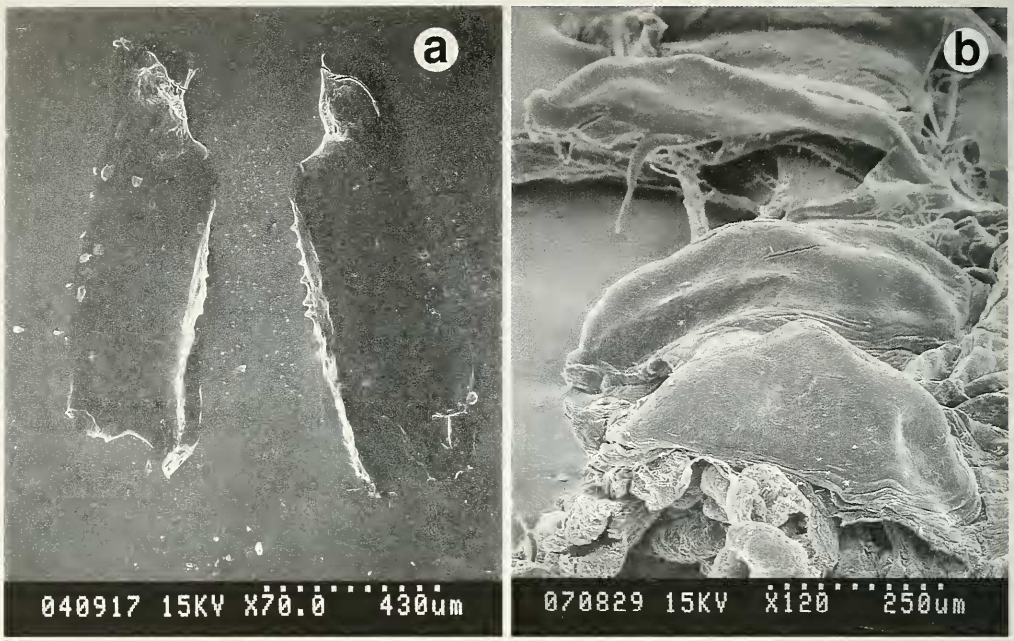

FIGURE 18. *Melibe rosea* Rang, 1829, digestive armature. A: Jaws. B: detail of stomach plates.

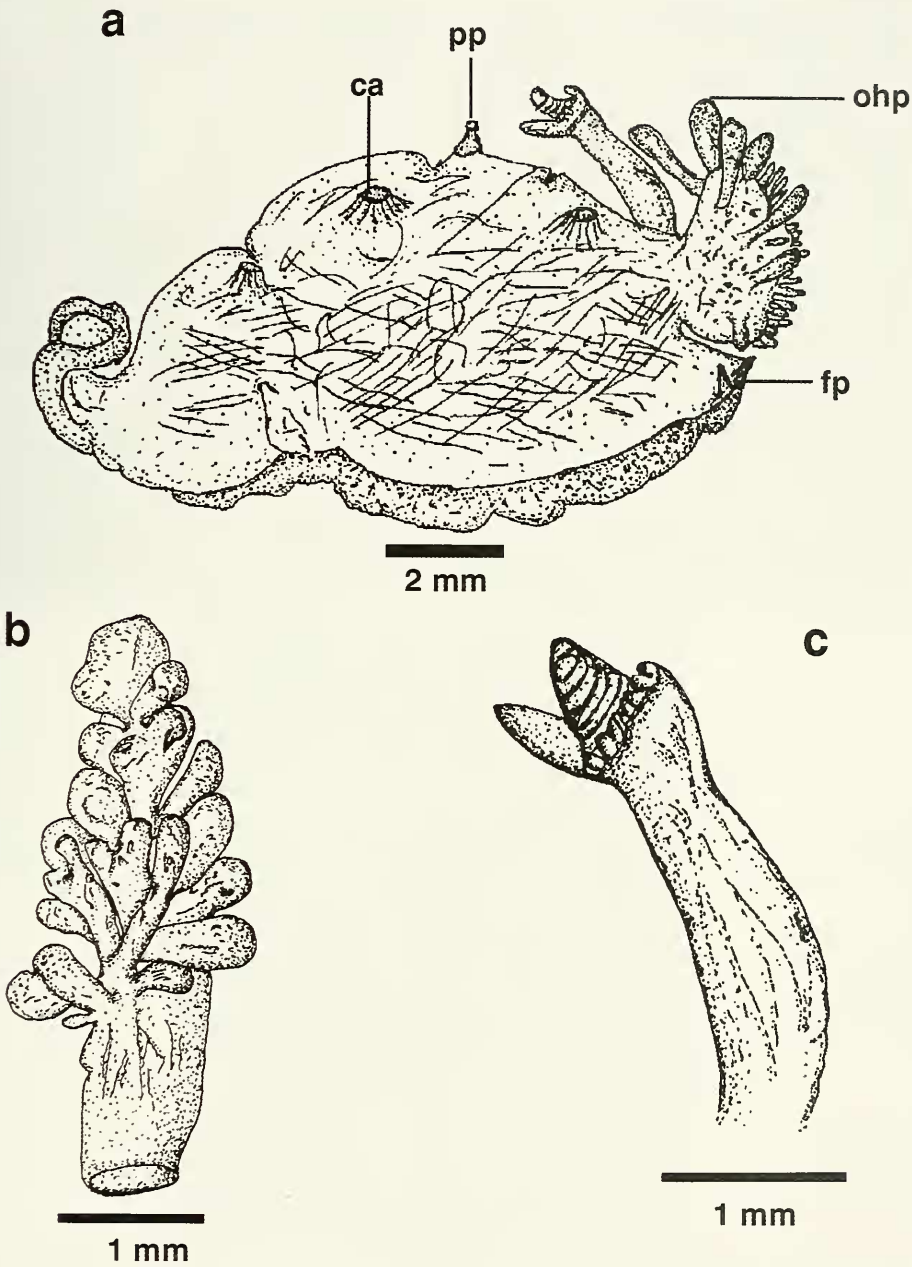

FIGURE 19. *Melibe tuberculata* sp. nov., external morphology. A: Body of preserved specimen without cerata (CASIZ 105639). B: detached ceras (CASIZ 106394). C: Detail of rhinophore (CASIZ 105639). Ca = point of ceratal attachment; fp = foot papillae, ohp = oral hood papillae; pp = unique papillae.

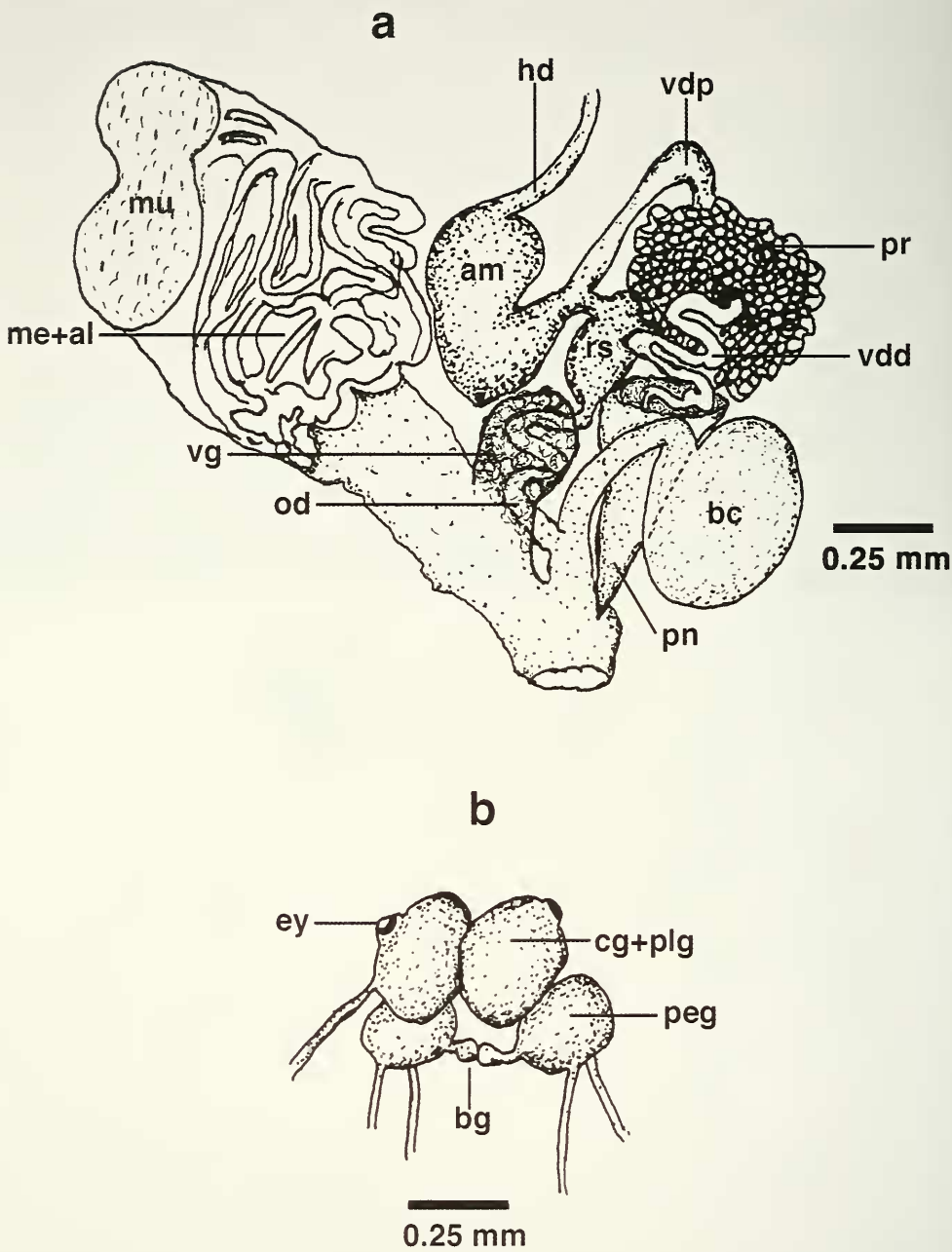

FIGURE 20. *Melibe tuberculata* sp. nov., anatomical details CASIZ 106394). A: Reproductive organs. B: Central nervous system. al = albumen gland; am = ampulla; bc = bursa copulatrix; bg = buccal ganglia; cg = cerebral ganglion; ey = eye; me = membrane gland; mu = mucous gland; od = oviduct; peg = pedal ganglion; plg = pleural ganglion; pn = penis. pr = prostate gland; rs = receptaculum semenis; vg = vaginal gland; vdd = distal vas deferens; vdp = proximal vas deferens.

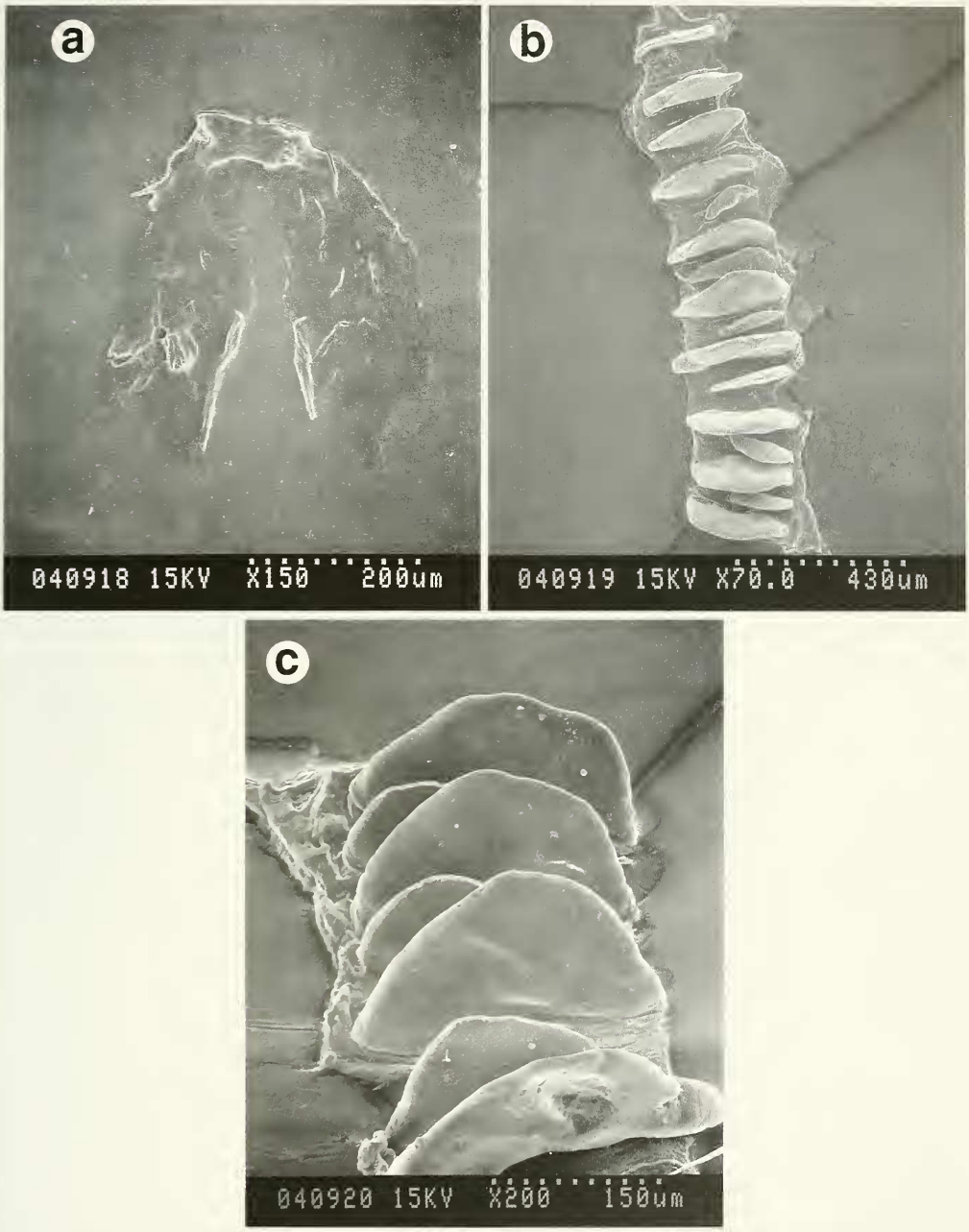

FIGURE 21. *Melibe tuberculata* sp. nov., digestive armature (CASIZ 106394). A: Jaws. B: Girdle of stomach plates. C: Detail of stomach plates.

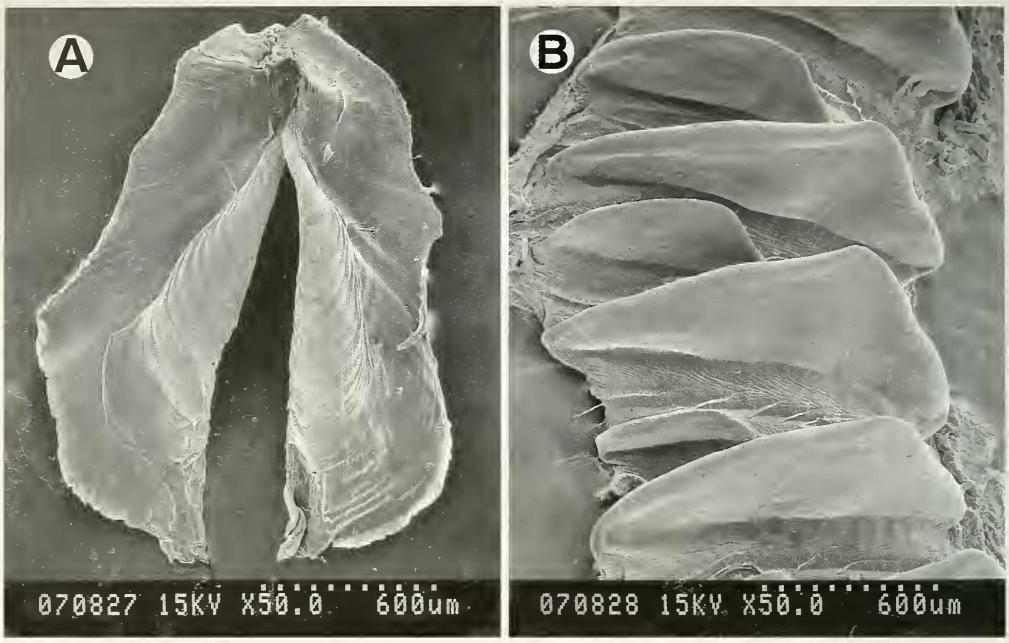

FIGURE 22. *Melibe viridis* (Kelaart, 1858). A: Jaws. B: Detail of stomach plates. C: Detail of ceras (CASIZ 83671).

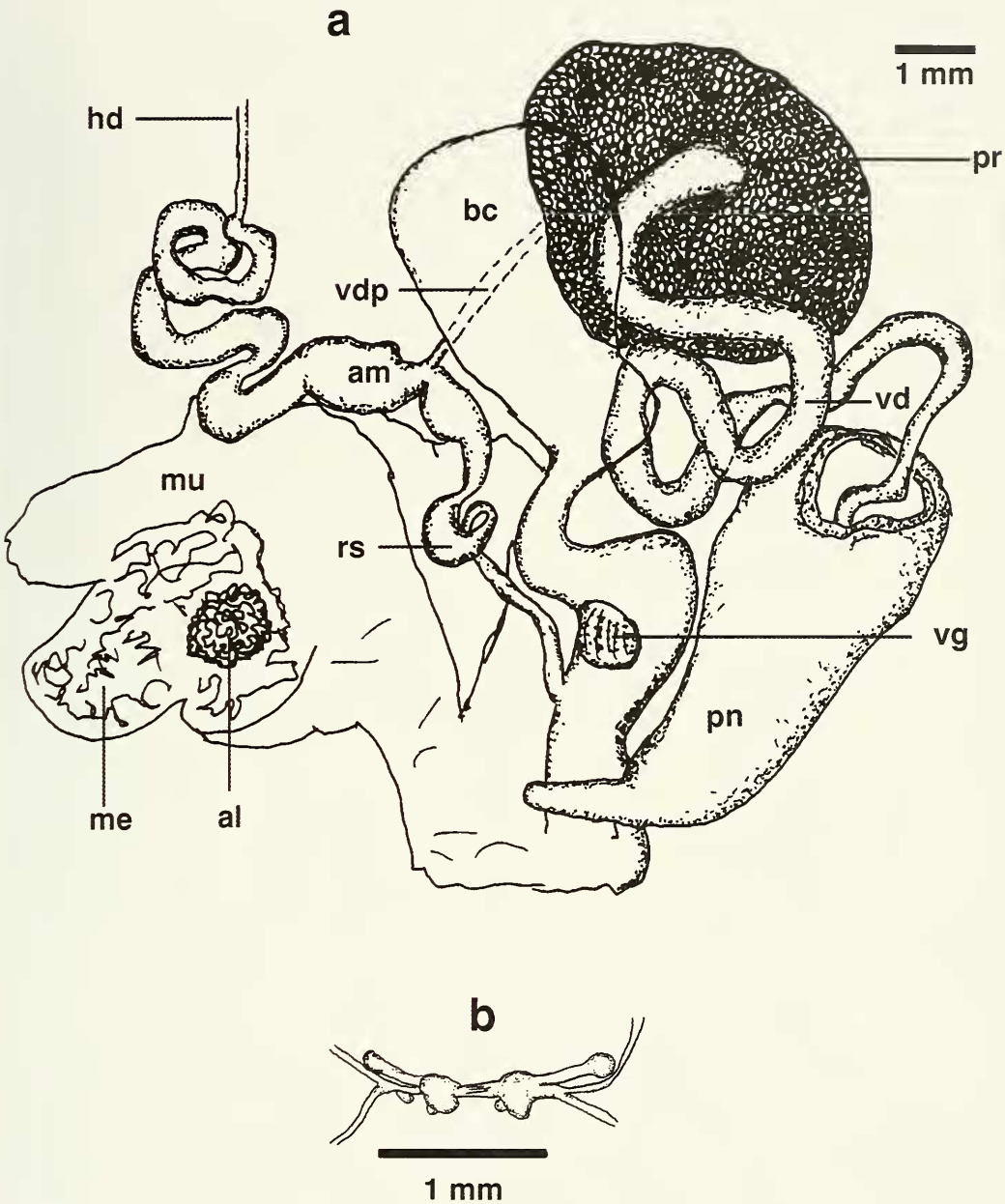

FIGURE 23. *Melibe viridis*, anatomy. A: Reproductive organs (composit drawing of CASIZ 61505 and 103727). B: Detail of buccal ganglia (CASIZ 83671). Al = albumen gland; am = ampulla; bc = bursa copulatrix; hd = hermaphroditic duct; me = membrane gland; mu = mucous gland; pn = penis; pr = prostate gland; rs = receptaculum semenis; vd = distal vas deferens; vdp = proximal vas deferens; vg = vaginal gland.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47
Marionia	2	1	0	0	2	?	?	?	0	0	0	0	0	?	?	?	0	?	0	0	0	1	0	2	0	0	0	0	2	2	0	2	0	0	1	1	0	2	2	2	?	1	0	0	0	0	0
Fimbria	0	1	0	1	0	2	1	0	0	1	0	0	1	0	0	0	0	0	0	0	2	1	0	5	?	?	?	0	0	0	0	3	0	0	1	1	0	2	2	2	?	1	0	1	0	1	0
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leonina	0	1	0	1	0	1	2	0	0	1	0	1	1	1	0	0	0	0	0	0	2	0	0	3	?	?	?	1	0	1	0	3	1	0	1	1	0	0	0	1	0	1	0	1	2	0	0
liltvedi	2	1	0	1	0	2	1	0	0	0	1	1	1	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	3	0	0	1	2	0	2	2	0	?	1	0	1	0	0	0
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rosea	2	1	0	1	0	2	1	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	1	2	0	2	2	0	?	0	0	1	0	0	0
tuberculata	0	0	1	1	1	1	0	1	1	0	1	1	1	0	0	1	0	1	1	0	1	0	1	1	1	0	1	1	1	1	1	3	0	0	0	0	0	1	1	1	1	0	2	1	0	0	1
viridis	1	1	0	1	0	2	1	1	0	0	1	1	1	1	1	1	1	2	1	0	1	0	0	2	1	1	1	1	1	1	0	0	1	0	1	2	1	2	0	1	0	1	1	1	0	0	1

FIGURE 24. Matrix of species and characters used in phylogenetic analysis

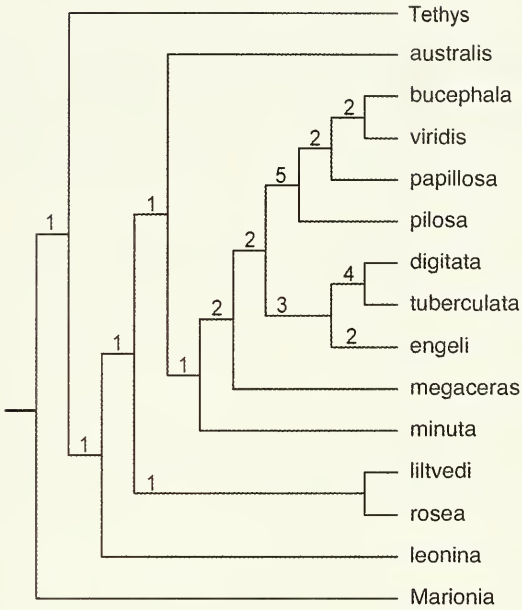

FIGURE 25. Tree resulting from phylogenetic analysis of data. Bremer support values shown at nodes.